2013

Chapter 4 Biological consequences for Landslide Ecology

Lawrence R. Walker
University of Nevada, walker@unlv.nevada.edu

Aaron B. Shiels
USDA/APHIS/WS National Wildlife Research Center, Aaron.B.Shiels@aphis.usda.gov

Published in LANDSLIDE ECOLOGY (New York: Cambridge University Press, 2013), by Lawrence R. Walker (University of Nevada, Las Vegas) and Aaron B. Shiels (USDA National Wildlife Research Center, Hila, Hawai'i).

4 · *Biological consequences*

Key points

1. Landslide colonists have adaptations to survive low-nutrient, unstable substrates, where they may also experience temperature and water stress. Many of the species that colonize landslides are found exclusively in disturbed habitats and are known as gap specialists. Other colonists are common species in the adjacent undisturbed environment where their proximity to the landslide may have enabled rapid dispersal.
2. Microbes (including bacteria and fungi) are probably the first organisms to disperse to and colonize landslides. Symbiotic relationships, such as lichens, and plants with mycorrhizal fungi or nitrogen fixing bacteria, represent adaptations for survival in newly exposed, low-nutrient landslide substrates.
3. All plant life forms are found on landslides, but tend to segregate by slope. Small plants including bryophytes and forbs tend to dominate steep slopes, while tree ferns and trees tend to dominate less steep slopes. Grasses, vines, vine-like scrambling ferns, and shrubs, as well as most wind-dispersed plants, are common colonists on many landslides.
4. Arthropods are typically the first animals to colonize landslides, and include mites, Collembola, and ants, which are well adapted to temperature extremes and drought conditions.
5. Vertebrates associated with landslides are generally visitors rather than residents of the landslides. Birds and small mammals are the most common visitors, yet most vertebrates do not visit landslides until sufficient ground cover or foraging material has become established.

4.1 Introduction

Landslides have much in common with many other types of disturbances because they result in gaps in the landscape vegetation that attract

organisms with life histories adapted to survival in such openings. However, landslides create unusual gaps because most of the physical structure is removed, and only bare, nutrient-poor substrates commonly remain. Treefalls also occur in many of the same forest environments as landslides, but treefalls generally disturb much smaller areas than landslides and result in gaps of mostly intact soils, often retaining the structural complexity of the understory (Reagan & Waide, 1996). Because of the physical consequences of the disturbance, landslides initially have a negative effect on biota. However, the loss of biomass and species creates opportunities for species that are not typically present or abundant in undisturbed habitats. Like any patch that has experienced a disturbance, a range of organisms with different morphological and ecological attributes can colonize a landslide as it undergoes successional change (see Chapter 5). The diversity of organisms that occupy a landslide is therefore partly influenced by the mode of arrival (e.g., wind vs. animal dispersal) and timing (e.g., early vs. late in succession). Following its arrival, an organism's length of stay on a landslide can also vary; species well adapted to minimizing water loss and temperature stress can become established and dominate for decades (e.g., ants and scrambling ferns in tropical landslides), whereas others such as forest birds might visit landslides for mere seconds to forage.

This chapter begins by describing how organisms are dispersed into landslides and outlines some of the general adaptations that allow such organisms to colonize successfully. We then focus on behaviors and adaptations of specific groups of organisms that colonize tropical and temperate landslides, including bacteria, fungi, lichens, bryophytes, ferns, gymnosperms, grasses, forbs, woody angiosperms, invertebrates, and vertebrates.

4.2 Dispersal

The conditions in gaps created by landslides can present strong barriers to potential colonists. Remnant patches of vegetation and soil, if present at all, represent a minor portion of the landslide. Therefore, landslide-colonizing organisms must generally have been dispersed from outside the landslide gap (exogenous propagules). In contrast, dispersal into a treefall gap can occur from sources within the gap because the soil seed bank and understory vegetation remain largely intact. Exogenous propagules (e.g., spores, seeds, plant parts, larvae, eggs) are transported to landslides

passively by gravity, wind, water, or animals, or actively by their own motility (e.g., worms, insects).

Many propagules, including a suite of microorganisms (e.g., bacteria, fungi, nematodes, protozoa, rotifers, and mites), are dispersed into landslides from the edges while attached to or incorporated within roots, rocks, soil, and organic matter. Despite the presence of appendages used for walking and crawling, most microfauna (< 0.1 mm in size) and mesofauna (0.1–2.0 mm) typically spend their entire lives within a square meter of soil (Coleman *et al.*, 2004). Macrofauna (> 2 mm; earthworms, spiders, pill bugs, beetles, slugs, snails, and ants) are generally more mobile than smaller organisms and are therefore more likely to disperse into landslides on their own accord. All of these invertebrates can potentially faciliate establishment of plants and other organisms through their effects on soil development and nutrient cycling during early primary succession (Hodkinson *et al.*, 2002).

The distribution of plant propagules from parent sources is directly influenced by distance, and most species have limited dispersal distances (Malanson & Cairns, 1997; Fenner & Thompson, 2005). Therefore, landslide size affects the dispersal of propagules into a landslide because of the positive relationship between area and edge-to-center distance (Miles *et al.*, 1984). Many conditions in landslide environments, including the abundance of propagules, vary spatially along an edge-to-center gradient (see Chapter 2). On two tropical landslides, Walker & Neris (1993) found that seed rain (numbers of seeds m^{-2}) tended to increase from landslide interior to edge, and was highest in the surrounding forest. However, the number of seeds deposited into a landslide can reach annual levels from tens to thousands of individuals m^{-2} for small-seeded species such as graminoids (Shiels & Walker, 2003) and Asteraceae (Dale, 1986; Myster & Sarmiento, 1998). These initial landslide colonists greatly influence subsequent seed dispersal and the spread of vegetation within the landslide. Small-seeded, wind-dispersed seeds were the dominant types dispersed to landslides in Japan (Nakashizuka *et al.*, 1993), Ecuador (Myster & Sarmiento, 1998), and Puerto Rico (Shiels & Walker, 2003), a pattern typical of early successional plants (Fenner & Thompson, 2005). However, the likelihood of wind dispersal into a gap is strongly influenced by the environment, including the distance to parent plants, the height of the seeds on the parent plants, the height and density of surrounding vegetation, and proximal weather conditions (Fenner & Thompson, 2005). Larger seeds therefore face a greater barrier to dispersal to landslides than

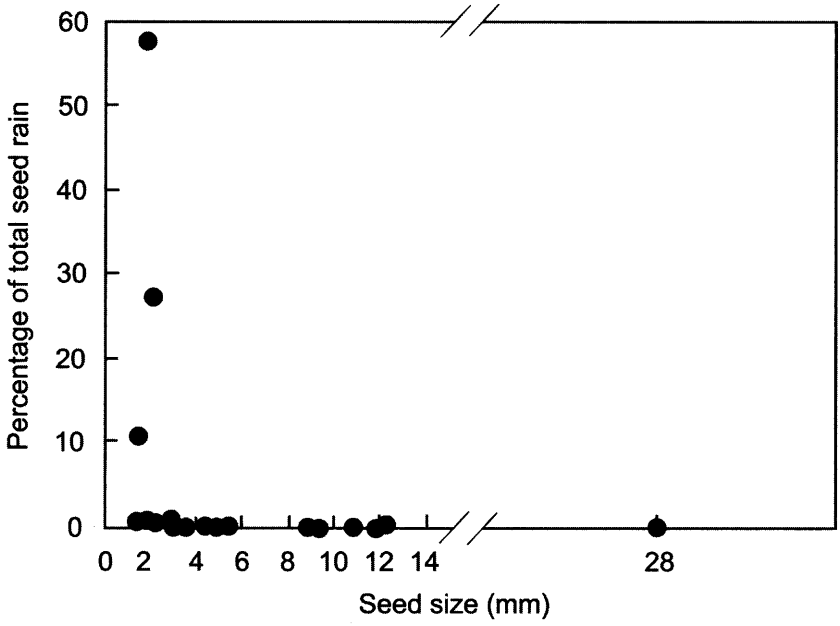

Fig. 4.1. The percentage of seed rain of various seed sizes collected over 14 months in six young (< 6 year old) landslides in the Luquillo Mountains, Puerto Rico. Three graminoids (two grass species, *Andropogon bicornis* and *Paspalum conjugatum*, and one sedge species, *Rhyncospora holoschoenoides*) comprised > 95% of the seed rain when all six landslides were combined. Seeds > 2.2 mm in longest axial length were rarely trapped in these recent landslides unless artificial perches were present. Seed traps excluded all spores and seeds < 1 mm in longest axial length. Seed rain data were taken from Shiels & Walker (2003) and excluded seed traps beneath artificial perches. The largest seed shown (28 mm; tabonuco tree, *Dacryodes excelsa*) represents one of the dominant tree species in the forest and it, like most mid- and late-successional species (many not shown), was largely absent from the landslide seed rain.

do smaller seeds, and larger seeds are often adapted to dispersal by animals (Parendes & Jones, 2000; Shiels & Walker, 2003; Matt *et al.*, 2008). The vast majority of seeds dispersed into six relatively young landslides in Puerto Rico were wind-dispersed grasses and sedges, each of which had small seeds that were $\leq$ 2.2 mm in longest axial length (Fig. 4.1). Seeds that blow into landslides can also be trapped by foliage of already established plants, which may provide amenable conditions (e.g., increased shade and soil moisture) for germination (Dale, 1986). In addition to seed rain, seed plant dispersal into landslides may be concentrated at the edges due to secondary erosion from the edge, which can frequently

deposit both seeds and other plant propagules (e.g., roots, rhizomes, seedlings) into the landslide (Dale, 1986).

Non-seed plants such as bryophytes and ferns are also common on landslides, and the small, bouyant, and abundant nature of their spores promotes dispersal (Walker & Sharpe, 2010). Although spore-bearing structures (e.g., sporocarps, sporophylls) are commonly elevated on spore-bearing plants, most of the non-seed plants remain low to the ground relative to shrubs and trees. Spore-bearing tree ferns are an exception, sometimes reaching heights of 20 m (Large & Braggins, 2004). Tree ferns colonize landslides across their range in some temperate forests (mainly in the Southern Hemisphere) and many subtropical and tropical forests (Mark *et al.*, 1964; Walker & Sharpe, 2010). Spore-rain produced by landslide-colonizing tree ferns from the genus *Cyathea* in Puerto Rico can reach 3–5 billion spores annually from a single leaf (Conant, 1976), whereas a single leaf of a different *Cyathea* species was reported to produce 600 million spores in 1 year (Tryon & Tryon, 1982). Myster & Fernández (1995) estimated that *Cyathea* (likely *C. arborea*) spore rain over a period of 2 months on 6 to 20 year old landslides in Puerto Rico was approximately 700 spores m^{-2}. Spores readily travel by wind and can survive transport over thousands of kilometers in large air masses including jet streams (Punetha, 1991; Kessler, 2010). Fern dispersal patterns are similar to those of seed plants because most fern spores are deposited in close proximity to the parent plant. For example, an 8 m tall Puerto Rican *Cyathea arborea* deposited most spores within 7.5 m of the parent plant, yet some spores were recovered 30 m away (Conant, 1976). Roads, powerline tracts, and other gaps provide corridors that likely enhance dispersal distances of spore- and seed-bearing plants that rely upon wind dispersal (Parendes & Jones, 2000). Even in forests where spore disperal may be limited by physical interference from tall trees, spore-bearing plants such as ferns apparently disperse well, as shown by their dominance on many tropical landslides in early stages of succession (Walker, 1994; Walker & Sharpe, 2010). Differences in air temperature between landslides and adjacent vegetated surroundings may also affect spore dispersal. Spore dispersal into landslides may increase when lower nighttime temperatues lead to sinking air masses over landslides. Enhanced spore dispersal may also result from warm daytime temperatures in landslides creating ascending air that lofts spores released from landslide colonists high into the atmosphere (Ricklefs *et al.*, 1995). In addition to dispersal via wind, water can also transport spores and assist down slope colonization along sloped terrain. A combination of wind and water dispersal of spores may explain the

lichens, mosses, ferns, and fern allies (e.g., *Selaginella*) that grew from incubated landslide soils in Ecuador (Myster & Sarmiento, 1998).

Animals can play an important role in dispersing spores (McIlveen & Cole, 1976; Cázares & Trappe, 1994) and seeds (McDonnell & Stiles, 1983; Levey, 1988; Wunderle, 1997; Holl, 1998) into gaps, yet this process has received little study in the context of landslides. Soil-consuming fauna (e.g., earthworms, wasps, and birds that use mud for nest construction) may disperse fungal spores (McIlveen & Cole, 1976). Fecal pellets of many types of mammals are also likely sources of mycorrhizal spores and perhaps seeds of early successional plants (Cázares & Trappe, 1994; Janos *et al.*, 1995; Mangan & Adler, 1999). Ants are common dispersers of seeds in both arid (Fenner & Thompson, 2005) and mesic (Bryne & Levey, 1993) habitats, but whether ants disperse seeds to landslides is unknown. Birds are probably the most common vectors of animal-assisted seed dispersal (zoochory) into landslides. In Puerto Rico, addition of artificial perches increased the dispersal of several species of forest seeds (Fig. 4.2). Dispersal mechanisms included both gut-passage for small seeds, as well as regurgitation for larger seeds (Shiels & Walker, 2003). Mammals can also be important vectors of seed dispersal into landslides. Like birds, frugivorous bats may fly through landslides but will not likely stop within the landslide unless perches (usually > 5 m tall) are present (M. Gannon, pers. commun.). Bats are particularly important dispersers of seeds into tropical landslides (Matt *et al.*, 2008). Bat droppings that contained hundreds of *Cecropia schreberiana* seeds were found in seed traps on an old (> 50 year) landslide with trees > 10 m tall in Puerto Rico (A. Shiels, pers. obs.). In addition to *C. schreberiana*, several species of gap-colonizing *Piper* are bat-dispersed in Puerto Rico (Devoe, 1989). In Mexico, two opposums (*Philander opossum* and *Didelphis marsupialis*) dispersed landslide-colonizing *Cecropia obtusifolia* as far as 70 m from a source plant (Medellin, 1994). Rats also disperse seeds into landslides. In seed traps on several relatively recent (< 6 year) Puerto Rican landslides, Shiels (2002) frequently found droppings of introduced black rats (*Rattus rattus*) that each contained tens to hundreds of seeds of native *Miconia* spp. The prevalence of non-native *Miconia calvescens* on some Pacific Island landslides may also be partly due to black rats dispersing the small seeds (Meyer & Florence, 1996; Shiels, 2011). Larger mammals such as monkeys may disperse seeds and spores into landslides. For example, 42% of the diets of Afro-montane monkeys (*Circopithecus l'hoesti*) in a forest in Rwanda included fruits and seeds, at least two species of fern fronds were consumed, and the monkeys commonly visited landslides to forage,

Fig. 4.2. Bird perches (5 m tall saplings) erected on Puerto Rican landslides to encourage bird visitation and seed dispersal of forest species. Photograph by A.B. Shiels.

socialize, rest, and scan (Kaplan & Moermond, 2000). Ungulates can also disperse seeds and spores into landslides following direct consumption and gut passage or by attachment of seeds and spores to the outside of the animal (epizoochory). Members of the genus *Desmodium* are epizoochorous forbs that colonize landslides in Hawaii (Restrepo & Vitousek, 2001), Nicaragua (Velázquez & Gómez-Sal, 2007), and Puerto Rico (Shiels & Walker, 2003), where birds or mammals are probably responsible for their dispersal. Similarly, there are two species of sedges (*Uncinia* spp.) found on landslides in Fiordland, New Zealand that are likely dispersed by epizoochory (Mark *et al.*, 1964). Seed dispersal to landslides by mammals is probably underestimated due to the fleeting nature of mammalian passage through such habitats, as well as the nocturnal habits and unobtrusive feces of many mammals. A variety of invertebrates and vertebrates may disperse spores and seeds into landslides. For any given species of plant or microbe, there are typically multiple mechanisms enabling propagules to reach and colonize disturbed sites (Pakeman *et al.*, 1998).

4.3 Colonization and species adaptations

Colonization reflects the ability of an organism to tolerate and survive the conditions of a landslide. For plants, colonization is defined as survival through germination and establishment; thus, the seeds of seed plants must germinate and establish true leaves (i.e., survive the cotyledon stage), the spores of bryophytes must germinate and produce a gametophyte, while ferns must survive the gametophyte phase and produce a leafy sporophyte. For animals and microorganisms, colonization simply reflects survival while in the landslide, and we therefore do not distinguish dispersal from colonization for animals and microbes. An animal visitation to a landslide, for example, can be considered a colonization event. In terms of the number of individuals and species, the successful colonists are a subset of those organisms dispersed into a landslide. Studies of plants on landslides highlight the survival barrier between dispersal and colonization (Dale, 1986; Walker & Neris, 1993; Shiels & Walker, 2003). Clearly, there are many species that lack the necessary adaptations to survive within the landslide environment.

Landslide colonists are largely species that are well adapted to tolerate water and temperature stress (Lundgren, 1978; García-Fayos *et al.*, 2000). Species that are only found in landslides, known as landslide specialists, apparently do not exist (Box 4.1); yet many of the species that colonize landslides are found exclusively in disturbed habitats

Box 4.1 Landslide specialists

Successful landslide colonists have dispersal and colonization characteristics that favor survival on relatively bare, sloped terrain, as well as conditions of high light, extreme temperatures, and water and nutrient stress. A landslide specialist is a species unique to landslides and otherwise absent in all other types of environments. We know of no such species that are only found on landslides. This may not be surprising because landslides are relatively random events and specialization requires long-term adaptations to specific conditions. If a landslide specialist did exist, it would require a landscape that experienced frequent landslides that essentially supported the characteristics of the specialist. Specialists are fragile because they can lead to evolutionary dead-ends if, for example, available landslide habitat becomes rare or unavailable. One example of specialization to landslide habitats that occurs within a species is evident for the pioneer tropical tree *Trema micrantha*. Recent work has shown some morphological distinctions (e.g., seed and leaf size), as well as functional differences in growth responses to nutrients, mycorrhizae, and herbivory, between landslide morphotypes relative to treefall gap morphotypes (Silvera *et al.*, 2003; Pizano *et al.*, 2011). Genetic comparisons between the morphotypes would help explain the extent to which such traits may be genetically fixed, yet this example with *T. micrantha* highlights the extent to which landslide colonizing species adjust to landslide conditions. Although landslide specialists (species level) may not exist, gap specialists are common colonizers of landslides. Gap specialists are organisms that are only found in disturbed habitats such as forest gaps (Denslow, 1980). Some of the gap specialists that are found in landslides include lichens with members in the genus *Stereocaulon* (see Section 4.4), scrambling ferns in the Gleicheniaceae (see Section 4.5.2), many representatives in the grass family Poaceae (see Section 4.5.4), the pioneer tree species in the genera *Alnus* and *Cecropia* (see Section 4.5.6), and *Wasmannia auropunctata* fire ants (see Section 4.6.1). Pikas (*Ochotona princeps*) live in talus environments formed by rock falls or landslides (Hafner, 1993). Several characteristics of the landslide environment (e.g., size, age, exposed rock, cracks in substrate, remnant soils or biota) influence the composition of the colonizing community and its similarity to or difference from that of other types of non-landslide disturbances, including the presence of gap specialists.

(gap specialists), and some species have morphological and/or functional adaptations that distinguish landslide morphotypes from other morphotypes found in disturbed habitats such as treefall gaps (e.g., *Trema micrantha* in Panama; Silvera *et al.*, 2003; Pizano *et al.*, 2011; Box 4.1). Species that colonize unstable or newly disturbed environments such as landslides tend to be categorized as pioneer or r-selected species, and they possess a suite of life-history characteristics that reflect adaptation to such unstable environments. Traits of r-selected species include high fecundity, small body (or seed) size, reduced time to reproduction, and the ability to disperse offspring widely. In contrast, K-selected species are those that are commonly found in stable environments, have low fecundity, large body size, a longer time to reproduction, and relatively poor dispersal (Townsend *et al.*, 2008). The r-selected life-history strategy is favored in environments such as landslides that allow for rapid population growth and expansion due to the initial presence of few individuals and few competitors.

4.3.1 Plant adaptations

There are several plant adaptations that favor colonization in the nutrient-poor landslide environment. To survive in low-nutrient substrates, some plants form symbiotic relationships with fungi (forming lichens, or mycorrhizal associations) and/or with nitrogen fixing bacteria in roots (see Section 4.4). Typical plant characteristics that aid survival in hot and dry environments include leaves that are reduced, dissected, thickened, waxy, hairy, or deciduous (Raven *et al.*, 2005). Each of these leaf adaptations helps to prevent water loss. Photosynthesis is a highly water-dependent process, and water stress on landslides may favor colonization by plants with water-efficient C_4 and CAM (crassulacean acid metabolism) pathways over less water-efficient C_3 plants, at least on tropical landslides (see Section 4.5.4).

4.3.2 Animal adaptations

Animals that successfully colonize landslides typically have small body sizes and structures and behaviors for increasing water retention. Some animals acquired traits long ago that improved their survival in dry and disturbed habitats; for example, during the Jurassic, insects evolved a waxy epicuticle, which enabled them to become day-active (Kronfeld-Schor & Dayan, 2003). This diurnal strategy may be altered in response to temperature and water stress. For example, in the Chihuahuan Desert,

ants (typical landslide colonists) foraged during the daytime in winter, whereas their summer foraging was restricted to nighttime and cloudy days (Whitford *et al.*, 1981). Other animals have behaviors that allow them to avoid environmental stresses on landslides by conducting short diurnal visits, visits around sunrise and sunset to avoid midday heat, and nocturnal visits. In Puerto Rico, the majority of observed bird visits to landslides were during the morning (A. Shiels, unpublished data); these visits were short (often just several seconds in duration, but averaging 1.1 minutes on artificial perches), and the birds typically returned to the cooler and more shaded confines of the nearby forest at the end of their landslide visit (Shiels & Walker, 2003). Many of the mammals that have been documented in landslides through sightings, tracks, or scat are nocturnal (see Section 4.2). Nocturnal activity in animals can often be linked to behavioral adaptations, such as avoidance of elevated daytime temperature and water loss in warm environments (Whitford *et al.*, 1981; Lourens & Nel, 1990; Kronfeld-Schor & Dayan, 2003). Nighttime temperatures in gaps are typically a few degrees cooler than adjacent non-gap environments, where the insulating properties associated with high vegetation cover create slightly warmer air temperatures. Cooler nighttime temperatures in gaps can potentially provide an accessible water source for animals in the form of dew (Richards, 2006), yet we know of no studies that have associated animal behaviors with nighttime water availability on landslides.

4.4 Bacteria, fungi, and lichens

Bacteria and fungi are important landslide colonists that often improve the nutrient conditions of the landslide through their metabolism, symbioses with other organisms, and role in decomposition and nutrient cycling. Although bacteria are prokaryotes and fungi are eukaryotes, they are discussed here in a single section because both are microscopic for all or part of their existence. Cyanobacteria, and several other types of bacteria, contain the enzyme nitrogenase, which allows them to convert atmospheric nitrogen to forms of nitrogen that are available for biotic uptake and use. Without bacteria providing such forms of nitrogen, plants (and other organisms which rely upon them) could not exist with their present physiology and biochemistry because they lack nitrogenase (Schlesinger, 1991).

Cyanobacteria (blue – green algae) are particularly well adapted to survival in harsh environments because they couple nitrogen fixation to their photosynthetic reaction. Organisms living closely with cyanobacteria

would therefore benefit from nitrogen availability, and for this reason, many types of cyanobacteria form symbioses with other organisms. One such interaction that occurs on several landslides is the symbiosis between a cyanobacteria (*Nostoc*) and plant species in the genus *Gunnera*. This unique interaction occurs when *Nostoc* enters the plant stem through specialized pores and initiates an intracellular symbiosis where the bacterium is thought to provide the plant with fixed nitrogen in return for fixed carbon from the plant (Bergman *et al.*, 1992). This symbiosis is particularly beneficial to plants that occupy nitrogen limited soils such as found on landslides (see Chapter 3). *Gunnera* is a gap-specialist (Palkovic, 1978), and it is found on landslides in several parts of the world, including New Zealand (Mark *et al.*, 1964), Chile (Veblen & Ashton, 1978), and Costa Rica, where it was the dominant plant species on two landslides (Myster, 1997).

The nitrogen fixing bacteria *Rhizobium* and *Frankia* are involved in symbioses with roots of several plant species, forming macroscopic nodules on the roots. This symbiosis represents yet another adaptation to nitrogen-deficient soils. Nodular nitrogen fixing symbionts colonize landslides frequently; their abundance on landslides (63%) resembles their abundance on mine tailings (64%) and floodplains (48%) but they are less frequent on other types of primary succession (Walker, 1993). Like the *Nostoc* – *Gunnera* symbiosis, *Rhizobium* or *Frankia* provide the plant with fixed nitrogen in return for fixed carbon. Many nodular nitrogen fixing symbioses involving *Rhizobium* and *Frankia* occur with plant colonists in temperate and tropical landslides (Table 4.1). *Rhizobium* has established nodular nitrogen fixing symbioses with most species in the Fabaceae, and with one genus in the Ulmaceae (Soltis *et al.*, 1995). *Rhizobium* is particularly well represented on landslides worldwide because of the relatively high incidence of Fabaceae in the landslide plant community. All other plants known to have nodular nitrogen fixing symbionts are associated with *Frankia*, including some genera from each of the following eight plant families: Betulaceae, Casuarinaceae, Coriariaceae, Elaeagnaceae, Datiscaceae, Myricaceae, Rhamnaceae, and Rosaceae (Soltis *et al.*, 1995). A variety of forbs, shrubs, and trees form nodular nitrogen fixing symbioses with *Rhizobium* or *Frankia* in landslides (Table 4.1).

Lichens are another symbiotic association between a fungus and a photosynthetic partner (green algae or cyanobacteria). Nitrogen fixation occurs in lichens when cyanobacteria (e.g., *Nostoc*) are involved as a symbiont. Lichens commonly colonize landslides and in some cases can be the dominant life form on portions of the landslide, such as the slip face

Table 4.1. *Plant species occurring on landslides that are from genera with nodular nitrogen fixing symbionts (cf. Schubert, 1986; Soltis* et al., *1995)*

Location	Species	Life form	Family	References
Temperate				
Queen Charlotte Islands, Canada	*Alnus rubra*	T	Betulaceae	Geertsema & Pojar, 2007
Montana Rocky Mountains, U.S.	*Alnus sinuata*	T	Betulaceae	Malanson & Butler, 1984
Mount St. Helens, U.S.	*Alnus rubra*	T	Betulaceae	Dale, 1986
	Lupinus latifolius	F	Fabaceae	
Alps, Switzerland	*Alnus viridis*	T	Betulaceae	Van der Burght *et al.*, 2012
Lake Thompson, New Zealand	*Coriaria arborea*	S	Coriariaceae	Mark *et al.*, 1964
Oregon Cascade Mountains, U.S.	*Alnus rubra*	T	Betulaceae	Miles & Swanson, 1986
	Ceanothus integerrimus	S	Rhamnaceae	
	Ceanothus velutinus	S	Rhamnaceae	
	Lotus purshiana	F	Fabaceae	
	Lotus micranthus	F	Fabaceae	
New Hampshire White Mountains, U.S.	*Alnus crispa*	T	Betulaceae	Flaccus, 1959
Andes Mountains, Argentina	*Coriaria ruscifolia*	S	Coriariaceae	Veblen & Ashton, 1978
	Lotus uliginosus	F	Fabaceae	
	Trifolium dubium	F	Fabaceae	
	Trifolium repens	F	Fabaceae	
Colorado Rocky Mountains, U.S.	*Lupinus sericeus*	S	Fabaceae	Langenheim, 1956
	Vicia americana	F	Fabaceae	
Virginia Appalachian Mountains, U.S.	*Robinia pseudoacacia*	T	Fabaceae	Hull & Scott, 1982
Mount Kiyosumi, Japan	*Albizia julibrissin*	T	Fabaceae	Sakai & Ohsawa, 1993
Flores Island, the Azores	*Lotus pedunculatus*	F	Fabaceae	Elias & Dias, 2009
Himalayan Mountains, Nepal	*Alnus nepalensis*	T	Betulaceae	Devkota *et al.*, 2006

(*cont.*)

Table 4.1. (cont.)

Location	Species	Life form	Family	References
Tropical				
Hawaii Koolau Mountains, U.S.	*Casuarina equisetifolia*	T	Casuarinaceae	Russo, 2005; A. Shiels, pers. obs.
Hawaii Mauna Loa Volcano, U.S.	*Desmodium* sp.	F	Fabaceae	Restrepo & Vitousek, 2001
Luquillo Mountains, Puerto Rico	*Desmodium incanum*	F	Fabaceae	Myster & Walker, 1997; Shiels & Walker, 2003
	Inga laurina	T	Fabaceae	
	Inga vera	T	Fabaceae	
Blue Mountains, Jamaica	*Myrica cerifera*	T	Myricaceae	Dalling, 1994
Andes Mountains, Bolivia	*Alnus acuminata*	T	Betulaceae	Kessler, 1999
Casita Volcano, Nicaragua	*Clitoria ternatea*	F	Fabaceae	Velázquez & Gómez-Sal, 2007, 2008, 2009b
	Calopogonium mucunoides	F	Fabaceae	
	Desmodium incanum	S	Fabaceae	
	Desmodium nicaraguense	S	Fabaceae	
	Galactia striata	F	Fabaceae	
	Mimosa pudica	F	Fabaceae	
	Stizolobium puriens	F	Fabaceae	
	Zornia thymifolia	F	Fabaceae	
Monteverde Cloud Forest, Costa Rica	*Pithecellobium costarricense*	T	Fabaceae	Myster, 1993
Uluguru Mountains, Tanzania	*Acacia mearnsii*	T	Fabaceae	Lundgren, 1978
	Crotalaria natalitia	F, S	Fabaceae	
	Eriosema psoraleoides	F	Fabaceae	
	Indigofera paniculata	F	Fabaceae	
	Myrica salicifolia	S, T	Myricaceae	
	Phaseolus vulgaris	F	Fabaceae	

Rhizobium is the prokaryote forming the symbiosis with representative taxa in Fabaceae, whereas *Frankia* is the prokaryote forming the symbiosis with all other taxa listed. Life forms are trees (T), shrubs (S), and forbs (F). References are indicative of the plant's presence on landslides and do not necessarily reflect confirmation of the presence or activity of nodular symbionts. Entries are listed in descending order by latitude for both temperate and tropical environments.

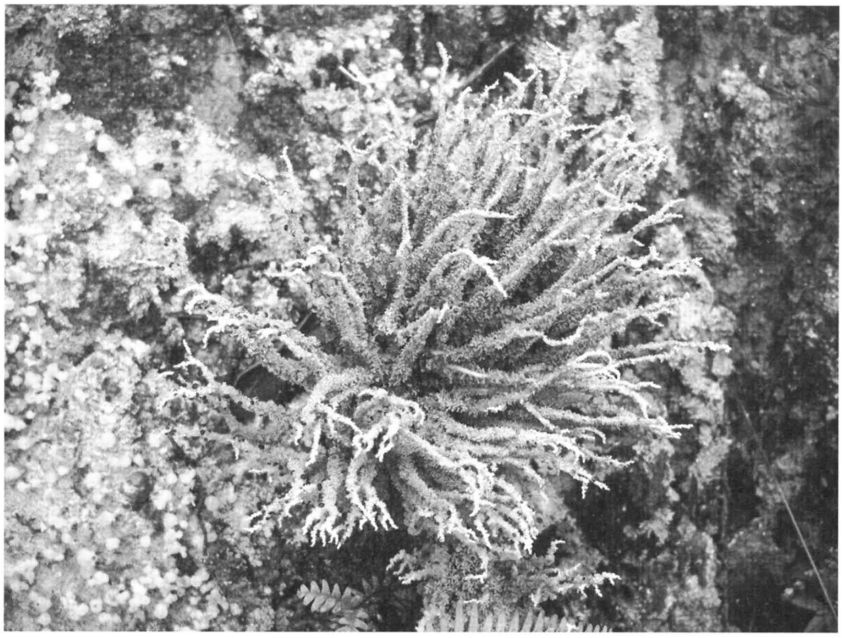

Fig. 4.3. A common lichen (*Stereocaulon virgatum*) on a Puerto Rican landslide. Photograph by A.B. Shiels. See also background of Plate 9.

or on rocks (Plate 9; Flaccus, 1959; Dalling, 1994). Unlike most plants, lichens do not require soil to establish and therefore lichens commonly colonize bare rock surfaces such as lava flows where they fix nitrogen (Vitousek, 1994); however, lichens were also found growing on incubated landslide soils in Ecuador (Myster & Sarmiento, 1998) and can occur on bark (Mark *et al.*, 1964). In Chile, lichens were found on approximately half of the earthquake-generated landslides sampled, and the microsites where lichens were most abundant were bedrock and rock debris (Veblen & Ashton, 1978). Lichens tend to be most common in early succession on steep slip faces and chutes and least common in deposition zones and on older landslides. For example, young landslides in Puerto Rico (< 1 year old; A. Shiels, pers. obs.), New Zealand (15 years; Mark *et al.*, 1964), Jamaica (15 years; Dalling, 1994), and Tanzania (3–7 years; Lundgren, 1978) had abundant lichen cover. *Stereocaulon virgatum*, for example, represented more than half of the landslide biomass in Jamaica (Dalling, 1994) and primarily inhabits exposed bedrock on landslides in Puerto Rico (Fig. 4.3; Plate 9). In some cases, lichens are present only on older landslides (19 and 35 years old but not 2 and 9 years old;

Flaccus, 1959), or present throughout a chronosequence of landslides (Mark *et al.*, 1964) or lava flows (Vitousek, 1994). Bacteria, fungi, and lichens can have disproportionally large and important effects on other organisms (e.g., plants) and processes such as decomposition and nitrogen cycling (see Chapter 3; Schlesinger, 1991; Coleman *et al.*, 2004). Their early colonization and symbiotic relationships with plants make them critical components of landslide recovery.

Free-living bacteria and fungi are also found in landslide soils, yet few surveys have been conducted that establish their relative abundances. Instead, total soil microbial biomass is more commonly sampled. Soil microbial biomass is greatly reduced by landslides. Arunachalam & Upadhyaya (2005) sampled soils over a short (4 year) landslide chronosequence in moist tropical deciduous forest in India, and found that there was 2–20 times more microbial biomass in the nearby forest than in any of the landslides sampled. Li *et al.* (2005) found that microbial biomass, and its constituent bacteria and fungi, were generally lower in two Puerto Rican landslides than in adjacent forest soils, and were lower on slip faces than deposition zones within the landslides. Soil fungi accounted for at least three times as much biomass as bacteria. There were no seasonal (wet vs. dry) differences in the soil bacteria biomass on landslides or in forest plots (Li *et al.*, 2005) but spatial variability was pronounced (see Chapter 2). Soil microbial biomass can be patchy in landslides, and it often correlates with soil carbon. Soil microbial heterogeneity was particularly pronounced in young landslides in India; some microsites in 6 month old landslides had ten times more microbial biomass than 4 year old landslides (Arunachalam & Upadhyaya, 2005). Experimental studies have shown that both bacteria and fungi have soil-binding properties that increase slope stability, and this effect is accentuated with fungi more than with bacteria because of the strand-like characteristics of the hyphae (Meadows *et al.*, 1994). Although the abundance of microbes may take many years to reach pre-landslide levels, the often immediate colonization of bacteria and fungi clearly plays an important role in plant species survival and succession.

Fungal infection can occur in both plants and animals that colonize landslides. Seeds of landslide colonists in Puerto Rico and Costa Rica were colonized by fungi and such infection (presumed to be pathogenic) correlated with greater seed loss than animal seed predation (Myster, 1997). The fungi inhabiting seeds on Puerto Rican landslides included species in the genera *Colletotrichum*, *Pythium*, *Arthrosporium*, and *Fusarium*, whereas the fungal taxa inhabiting seeds in Costa Rican landslides

were not identified (Myster, 1997). Fungi (species in the genera *Colletotrichum*, *Fusicladium*, *Phoma*, *Phyllachora*, *Phyllosticta*, and *Rhizoctonia*) also colonized leaves of early successional trees (*Cecropia schreberiana* and *Inga vera*) on two Puerto Rican landslides (Myster, 1997, 2002). The effects of the fungal infection on leaf area losses were minimal, and ranged from < 1% to 3% for both tree species (Myster, 2002). While the dispersal pathways of the fungal colonists were not apparent, dispersal via insects visiting the plants (de la Cruz & Dirzo, 1987) and wind dispersal were proposed as potential vectors of the plant-inhabiting fungi (Myster, 2002).

Mycorrhizal fungi may reside in landslides as symbionts with plants (Myster & Fernández, 1995; Fetcher *et al.*, 1996), or they may be present as dormant spores (Li *et al.*, 2005). Vesicular–arbuscular mycorrhizal fungi (VAM) were sampled on two Puerto Rican landslides, aged 6 years and 20 years, by examining fine-root infection frequency (Myster & Fernández, 1995). The majority (67%) of the landslide plots sampled, including all those in the upper slip face (top 40 m of the landslide), did not have any roots with VAM. The amount of VAM fungal colonization in root samples taken from within the landslide was never greater than 10%, whereas in the forest bordering the landslide there was typically 25% of the fine root length converted to VAM (Myster & Fernández, 1995). Therefore, even on relatively old landslides (one was 20 years old), VAM fungal colonization did not appear to recover to infection levels in the forest. The VAM genera that have colonized Puerto Rican landslides in the past include *Sclerocystis*, *Glomus*, and *Acaulospora* (D.J. Lodge, pers. comm.). Some landslide colonists studied in Puerto Rico do not appear to depend on mycorrhizal affiliations. *Cecropia schreberiana* did not show any positive growth when inoculated with VAM in landslide soils (Lodge & Calderon, unpublished data). However, both the facultatively mycorrhizal *C. schreberiana* and the non-mycorrhizal *Phytolacca rivinoides* showed positive spatial correlations with areas of high soil phosphorus availability on Puerto Rican landslides (Lodge & Calderon, unpublished data).

4.5 Plants

4.5.1 Bryophytes

Bryophytes, which include mosses, hornworts, and liverworts, are common at different stages of plant recovery on landslides (Plate 10). While bryophytes most commonly grow in moist environments, there are many

species that thrive in dry environments such as deserts and landslides (Tuba *et al.*, 2011). Bryophytes therefore occupy many of the same microhabitats as lichens. Their adaptations to landslides include spore dispersal and vegetative reproduction, the ability to withstand great fluctuations in temperature and moisture, and tolerance of a wide variety of abiotic and biotic substrates. Because bryophytes often harbor cyanobacteria and fungi (that aid in the acquisition of nutrients; Raven *et al.*, 2005), they are also potentially adapted to low-nutrient landslide soils.

Bryophyte frequency, cover, and biomass can all be substantial on temperate landslides. On landslides triggered by earthquakes in Chile in 1960, bryophytes were recorded on 50%–100% of all plots (Veblen & Ashton, 1978). In New Zealand, Mark *et al.* (1964) documented bryophytes on both the ground and as epiphytes along a 78 year old landslide chronosequence. On the ground, bryophyte cover decreased through succession and was most prevalent on the slip face of the 15 year old landslides where its biomass was nearly double that of the bryophytes inhabiting the ground in the nearby forest (Mark *et al.*, 1964). In contrast, epiphytic bryophytes were more common as succession proceeded. Typical genera included *Macromitrium* and *Weymouthia* (mosses), and *Metzgeria*, *Porella*, and *Radula* (liverworts) (Mark *et al.*, 1964). Other genera found on temperate landslides include *Sphagnum* and *Polytrichum* mosses. *Sphagnum* covers more than 1% of the Earth's surface (Raven *et al.*, 2005), and in the Azores, *Sphagnum* spp. was the dominant or co-dominant plant in the upper (slip face) portion of young, intermediate, and old landslides (Elias & Dias, 2009). Blue–green algae are also found associated with *Sphagnum*, which can be an important source of fixed nitrogen in primary succession (Sheridan, 1991). *Polytrichum* spp. occurred on the upper parts of all ages of landslides sampled in the Azores, but its prevalence was greatest in the intermediate-aged landslides (representing 10%–15% cover; Elias & Dias, 2009). In New Hampshire, U.S., *Polytrichum* spp. occurred on 61% of all 9 year old landslides, making it the most frequently observed non-woody plant on these relatively young temperate landslides (Flaccus, 1959). The frequency of *Polytrichum* declined through succession, and it was only observed in 3% of the forest plots sampled. As a likely consequence of woody plant dominance later in succession, mosses were generally restricted to bare rocks and rock ledges in the 19 year old and 35 year old landslides (Flaccus, 1959).

Bryophyte studies on landslides are apparently less frequent in the tropics. However, mosses ranked second in total biomass on landslides in montane wet forest, Jamaica (Dalling, 1994). On 15 year old landslides,

bryophyte biomass was exceeded only by lichens, while on landslides > 50 years old, only woody plants had more biomass (Dalling, 1994). In Tanzania, bryophytes were only found near the perimeters of landslides where secondary erosion (e.g., sloughing) was common (Lundgren, 1978). Bryophytes are a substantial part of landslide vegetation, found mostly on slip faces and chutes, or anywhere that there are exposed rocks.

4.5.2 Ferns

Ferns are one of the most prominent plant life forms that colonize landslides in both temperate and tropical locations (Walker & Sharpe, 2010). Their success in disturbed environments is most likely due to the same adaptations listed for bryophytes above, plus the following: extensive rhizome growth, effective nutrient uptake or immobilization, a vertical, scrambling, or climbing life form, and rapid growth rates. We discuss the colonization of landslides by ferns and lycophytes (hereafter: ferns, as per ferns *sensu lato;* Mehltreter *et al.*, 2010), focusing on club mosses, horsetails, bracken, scrambling ferns, and tree ferns.

Club mosses (Lycopodiaceae) and horsetails (*Equisetum*; the only surviving genus in the Equisetaceae) dominated the vegetation of the Carboniferous Period and often grew to be tree-sized (Raven *et al.*, 2005). Their present-day relatives rarely exceed 50 cm in height. Both have adaptations to landslides that include small leaves, spore dispersal, and vegetative reproduction. Although club mosses can be outcompeted by scrambling ferns (e.g., Gleicheniaceae) and woody vegetation, Walker *et al.* (2010a) found that, when scrambling ferns were removed, club mosses (predominantly *Lycopodiella cernua*) dominated the vegetation on Puerto Rican landslides. Club mosses were also described on landslides in Jamaica where they comprised 3% of plant biomass (Dalling, 1994), and in New Zealand where they accounted for 25% of the vegetation cover on slip faces (Mark *et al.*, 1964). Horsetails can account for up to 20% of the cover of young landslides in Oregon (Miles & Swanson, 1986), Tanzania (Lundgren, 1978), Chile (Veblen & Ashton, 1978), and India (Arunachalam & Upadhyaya, 2005). Dominance by horsetails is likely to be only temporary, and it lasted only 4–7 years on landslides in Tanzania (Lundgren, 1978).

Pteridium aquilinum (bracken) is perhaps the most widespread fern on Earth, and it is a well-known colonist of disturbed sites (Walker & Sharpe, 2010). Kessler (1999) found that bracken was an important colonist of

landslides in Bolivia, but also noted that it did not reach densities in landslides as great as it did in most anthropogenic gaps. Bracken was also an important colonist of landslides in Tanzania where it appeared within 1 year of disturbance and persisted through 4 years (Lundgren, 1978). Part of bracken's post-establishment success in spreading may be due to vigorous vegetative reproduction via rhizomes. *Odontosoria aculeata* is in the same family as bracken (Dennstaedtiaceae) and it increased in cover after a fire swept through a landslide in Puerto Rico (Walker & Boneta, 1995). Aside from some grasses, *O. aculeata* represented the only plant surviving the fire, perhaps due to the abundance of partially buried rhizomes (Walker & Boneta, 1995). *Dennstaedtia punctilobula* is a temperate member of Dennstaedtiaceae that is known for rampant vegetative reproduction, and it was found on 68% of the plots among 22 landslides examined in the White Mountains, New Hampshire, U.S. (Flaccus, 1959).

A number of other fern genera comprise between 2% and 80% of vegetation cover on a particular landslide. Two of the most dominant genera reported were *Pityrogramma* and *Blechnum*. *Pityrogramma calomelanos* was a dominant colonist on tropical landslides on volcanoes in Nicaragua (Velázquez & Gómez-Sal, 2009b) and Mexico (Spicer *et al.*, 1985), and *P. ebenea* was found on landslides in Jamaica (Dalling, 1994). In the Azores, *Blechnum spicant* covered 3%–5% on young landslides but increased to 35%–75% on intermediate-aged landslides (Elias & Dias, 2009). In New Zealand, *Blechnum* spp. dominated the herbaceous layer of vegetation on slip faces (Mark *et al.*, 1964), yet the only *Blechnum* representative on Jamaican landslides (*B. lineatum*) was relatively uncommon (Dalling, 1994). Other fern genera commonly found on temperate landslides include *Dryopteris* in the Azores (Elias & Dias, 2009) and in New Hampshire (Flaccus, 1959), *Polystichum* in Oregon, U.S. (Miles & Swanson, 1986), and *Nephrolepis* in Hawaii, U.S. (Restrepo & Vitousek, 2001).

Scrambling ferns are tropical ferns with leaf tips that have indeterminate growth, branching rhizomes at the soil surface, and recumbent leaves that spread across the surface and over other vegetation (Walker & Sharpe, 2010). The most widespread scrambling ferns are in the Gleicheniaceae, and they often colonize disturbed habitats resulting from landslides, fires, and roads (Dalling, 1994; Walker & Boneta, 1995; Negishi *et al.*, 2006; see Fig. 5.5). In particular, species in this family are prominent on tropical landslides where they often form thickets that stabilize soils and competitively exclude other species (Walker, 1994; Russell *et al.*, 1998; Slocum *et al.*, 2004; Walker *et al.*, 2010a). *Dicranopteris curranii* colonized

roadside slopes in Malaysia, where it reduced water and sediment runoff and potentially ameliorated the ground layer microclimate by forming thickets (Negishi *et al.*, 2006). *Gleichenella pectinata* and *Sticherus bifidus* were also colonists of roadside landslides in Puerto Rico where they dominated the plant community for many years (Guariguata, 1990; Walker, 1994; Shiels & Walker, 2003). Similarly, on Oahu, Hawaii, *Dicranopteris linearis* was the dominant species for more than a decade after colonizing landslides with bare soils (Scott & Street, 1976). However, species in the Gleicheniaceae do not always form dominant thickets on landslides even when they are part of the local flora. For example, on the Island of Hawaii, Restrepo & Vitousek (2001) did not find *D. linearis* on their youngest landslides (4–42 years), but it was present on old landslides (approximately 130 years) and in forests (325–525 years). On intermediate-aged landslides in Bolivia where flowering plants dominated, *Sticherus* spp. and *Diplopterygium bancroftii* constituted 6%–12% of the vegetation cover, which was the highest among all ferns on all landslides sampled (Kessler, 1999). Interestingly, in the Blue Mountains of Jamaica, *Gleichenia jamaicensis* was absent from landslides > 50 years old, but present in relatively low abundances on three of the four 15 year old landslides that were sampled (Dalling, 1994).

Tree ferns are the largest ferns to colonize temperate and tropical landslides and they range in height from < 1 m to over 20 m (Plate 11; Large & Braggins, 2004; Walker & Sharpe, 2010). This height helps disperse their spores many meters from the parent (Conant, 1976; Tryon & Tryon, 1982; Myster & Fernández, 1995), thereby facilitating dispersal to and within landslides. Tree ferns have an erect rhizome (trunk or caudex) and occur in a number of families. Their taller stature and longevity can give them a competitive advantage over other ferns and seedlings, and sometimes they form monospecific stands on landslides (Walker *et al.*, 2010a; see Fig. 5.5). Although many tree ferns are good colonizers of landslides and grow rapidly (up to 40 or more cm $year^{-1}$; Walker & Aplet, 1994), they may also survive for decades to several centuries, becoming a part of the forest matrix (Tanner, 1983; Large & Braggins, 2004). Therefore, tree ferns can be present during some or all of the stages of landslide succession. For example, in Hawaii, *Sadleria pallida* was found on landslides of all ages sampled, yet *Cibotium glaucum* was only found on intermediate-aged (18–42 years) landslides (Restrepo & Vitousek, 2001). In the Azores, *Culcita macrocarpa*, which is apparently the only tree fern native to Europe, was found only on one old landslide (Elias & Dias, 2009). In Jamaica, two species of *Cyathea*

colonized several > 50 year old landslides, yet they had not colonized 15 year old landslides (Dalling, 1994). In Puerto Rico, *Cyathea arborea* is an important colonist of new landslides, but can also invade scrambling fern thickets, eventually displacing them, while inhibiting subsequent forest development (Walker *et al.*, 1996, 2010a). Tree fern trunks have additional ecological relevance as a substrate on which forest seedlings often germinate (Newton & Healey, 1989), thereby potentially increasing species diversity on landslides.

4.5.3 Gymnosperms

Seed plants are the dominant vegetation on many landslides in temperate and tropical ecosystems. Because of the initial paucity of animal colonists on landslides that are capable of dispersing seeds, most early landslide colonists have adaptations for wind-dispersal as well as many other traits of r-selected species that assist in colonizing landslide gaps (see Sections 4.2 and 4.3). Gymnosperms are seed plants that are more common on temperate than tropical landslides (Table 4.2). In some tropical areas prone to landslides, native gymnosperms are rare (e.g., Puerto Rico) or absent (e.g., Hawaii), but are sometimes planted to stabilize slopes (Acevedo-Rodríguez & Strong, 2005; A. Shiels, pers. obs.). Conifers are the most common form of gymnosperm found on temperate landslides and many are adapted for dispersal and colonization into disturbed areas including landslides, as shown by wind pollination, wind dispersal, and additional features of drought tolerance such as waxy, thickened leaves (Arno & Hammerly, 1984).

Douglas fir (*Pseudotsuga menziesii*) is the dominant conifer tree in forests on many western slopes of the Cascade Mountains in Oregon and Washington, U.S., and was the most common of 140 species of landslide colonists in that region (Miles *et al.*, 1984; Miles & Swanson, 1986), including a large landslide resulting from Mount St. Helen's eruption (Dale, 1986). *Larix decidua* colonized a large rockslide in Switzerland within 2 years and established dominance within 20 years (Van der Burght *et al.*, 2012). Despite these two examples, many conifers establish in landslides after angiosperms and non-seed plants provide shade or other habitat amelioration. For example, conifers dominated landslides that were at least 40 years old in both British Columbia (*Picea sitchensis* and *Tsuga heterophylla*; Geertsema & Pojar, 2007) and New Hampshire (*Picea rubens* and *Abies balsamea*; Flaccus, 1959). However, many conifers need exposure of mineral soil to germinate (Zasada *et al.*, 1992), so early

Table 4.2. *Dominant trees (both gymnosperms and angiosperms) documented in landslide studies*

Location	Species	Family	References
Temperate			
Queen Charlotte Islands, Canada	*Alnus rubra*	Betulaceae	Geertsema & Pojar, 2007
Montana Rocky Mountains, U.S.	*Populus tremuloides*	Salicaceae	Malanson & Butler, 1984
	Alnus sinuata	Betulaceae	
Mount St. Helens, U.S.	*Pseudotsuga menziesii*	Pinaceae	Dale, 1986
	Salix spp.	Salicaceae	
The Alps, Switzerland	*Larix decidua*	Pinaceae	Van der Burght *et al.*, 2012
	Betula pendula	Betulaceae	
Lake Thompson, New Zealand	*Leptospermum scoparium*	Myrtaceae	Mark *et al.*, 1964, 1989
	Aristotelia serrata	Elaeocarpaceae	
Oregon Cascade Mountains, U.S.	*Pseudotsuga menziesii*	Pinaceae	Miles *et al.*, 1984; Miles & Swanson, 1986
	Alnus rubra	Betulaceae	
New Hampshire White Mountains, U.S.	*Betula papyrifera*	Betulaceae	Flaccus, 1959
	Betula lutea	Betulaceae	
Matiri Valley, New Zealand	*Nothofagus fusca*	Nothofagaceae	Vittoz *et al.*, 2001
Andes Mountains, Argentina	*Nothofagus dombeyi*	Nothofagaceae	Veblen & Ashton, 1978
	Eucryphia cordifolia	Cunoniaceae	
Virginia Massanutten Mountain, U.S.	*Tsuga canadensis*	Pinaceae	Hupp, 1983
	Betula lenta	Betulaceae	
Virginia Appalachian Mountains, U.S.	*Liriodendron tulipifera*	Magnoliaceae	Hull & Scott, 1982
Waitakere Ranges, New Zealand	*Agathis australis*	Araucariaceae	Claessens *et al.*, 2006
Akaishi Mountains, Japan	*Salix bakko*	Salicaceae	Nakamura, 1984
	Carpinus japonica	Betulaceae	

(*cont.*)

Table 4.2. (cont.)

Location	Species	Family	References
Mt. Kiyosumi, Japan	*Euptelea polyandra*	Eupteleaceae	Sakai & Ohsawa, 1993
Flores Island, the Azores	*Juniperus brevifolia*	Cupressaceae	Elias & Dias, 2009
Himalayan Mountains, Nepal	*Alnus nepalensis*	Betulaceae	Devkota *et al.*, 2006
Himalayan Mountains, India	*Quercus* spp.	Betulaceae	Reddy & Singh, 1993
	Pinus roxburghii	Pinaceae	
Tropical			
Mauna Loa Volcano, Hawaii	*Metrosideros polymorpha*	Myrtaceae	Restrepo & Vitousek, 2001
Luquillo Mountains, Puerto Rico	*Cecropia schreberiana*	Cecropiaceae	Myster & Walker, 1997
	Psychotria berteriana	Rubiaceae	
Blue Mountains, Jamaica	*Clethra occidentalis*	Clethraceae	Dalling, 1994
Casita Volcano, Nicaragua	*Trema micrantha*	Cannabaceae	Velázquez & Gómez-Sal, 2008
	Muntingia calabura	Muntingiaceae	
Monteverde Cloud Forest, Costa Rica	*Palicourea standleyana*	Rubiaceae	Myster, 1997
	Cecropia polyphlebia	Cecropiaceae	
Darien Province, Panama	*Trema micrantha*	Cannabaceae	Garwood *et al.*, 1979

Dominance was based on stem abundance, frequency, biomass, or cover, and included one to many landslides. Entries are listed in descending order by latitude within both temperate and tropical categories. When more than one species is listed for a location, the most common species is listed first. All studies were conducted in forests or forest–farmland habitats.

succession on landslides can be optimal for their establishment (e.g., *Pinus roxburghii* in the Himalayas; Reddy & Singh, 1993). In a study in the Azores, different morphological forms of the same species were found at different stages of landslide development. While some *Juniperus brevifolia* seedlings colonized the most recent landslides (those without any soil), the shrub form of *J. brevifolia* expanded to 25%–50% of total vegetation cover on intermediate-aged landslides, and *J. brevifolia* trees dominated the oldest landslides (Elias & Dias, 2009).

In the southern hemisphere, conifers in the family Araucariaceae occupy landslides in both temperate Argentina and New Zealand (Table 4.2; Plate 12; Veblen & Ashton, 1978; Claessens *et al.*, 2006). Additionally, Denslow (1980) classified several species of Araucariaceae as gap specialists in New Zealand, Solomon Islands, and New Guinea. In New Zealand, regeneration of kauri trees (*Agathis australis*) appears to depend on landslides or treefall gaps (Claessens *et al.*, 2006). Using landscape modeling techniques, Claessens *et al.* (2006) determined that mature kauri trees tend to occur on sites with moderate to high landslide hazard in northern New Zealand. Furthermore, mature kauri trees have a positive feedback on retaining kauri dominance in a patch; upon death of a mature kauri through wind damage or a landslide, increased light from the newly formed gap promotes kauri seedling regeneration (Claessens *et al.*, 2006). The presence of conifers such as *A. australis* can help identify past landslides as well as help predict future landslides. However, other types of conifer-dominated vegetation on landslides, featuring such species as *Pseudotsuga menziesii* in the Pacific Northwest (U.S.) and *Juniperus brevifolia* in the Azores, resemble the adjacent, less-disturbed forest and therefore the landslide may only be discernible from the forest by reduced plant size and a uniform age class structure (Elias & Dias, 2009). Conifers may therefore be a dominant feature of landslides at all stages of succession, although some are gap specialists.

4.5.4 Grasses

Grasses represent one of the most successful groups of plants on the planet, and they can rapidly colonize and dominate landslides for several years following disturbance (Velázquez & Gómez-Sal, 2009b). Key features of grasses that colonize landslides include: pollination and dispersal adaptations to dry habitats, extensive fine-root systems, frequent vegetative reproduction, leaf adaptations to discourage herbivory and limit water loss, relatively high incidence of C_4 photosynthesis, rapid growth, and

short periods to reproduction (Raven *et al.*, 2005). Like gymnosperms, grass pollination generally occurs by wind and therefore the open and often dry landslide environment likely aids in reproduction of early grass colonizers. Grasses often produce hundreds of seeds on a single plant and some have accessories to aid in wind dispersal. For example, species in the genus *Andropogon* have hairy spikelets that help dispersal by wind and they are common landslide colonists in Puerto Rico (Walker & Boneta, 1995; Shiels & Walker, 2003), Hawaii (Restrepo & Vitousek, 2001), and Ecuador (Myster & Sarmiento, 1998). However, many other grasses do not have hairs or other accessories to help with movement via wind but instead (like spore-bearing plants) rely on their small size. The fruit of a grass is a caryopsis, which is dry and fused to the seed coat, and it generally allows the seeds to be moved easily by the wind. Most landslide colonists that are grasses do have small (< 3 mm in length) seeds in both temperate (Flaccus, 1959; Veblen & Ashton, 1978; Miles & Swanson, 1986) and tropical (Lundgren, 1978; Restrepo & Vitousek, 2001; Shiels & Walker, 2003) environments.

The extensive, fine-root systems of grasses help stabilize soils and improve water and nutrient uptake, which is an advantage on unstable, dry, nutrient-poor landslides. Nutrient-poor landslides support increased root growth compared to roots on more fertile landslides (Walker & Shiels, 2008). Landslide soils are also not readily colonized by mycorrhizal fungi (Shaw & Sidle, 1983; Guariguata, 1990; Myster & Fernández, 1995), but the frequent absence of mycorrhizae in landslides can provide a competitive advantage to plants that have fine root systems for nutrient uptake, such as grasses (Lambers *et al.*, 1998). Microsites where rooting is possible on landslides can also be limited, especially in the slip face and chute where exposed bedrock or shallow soils predominate (see Chapter 3; Adams & Sidle, 1987; Sakai & Ohsawa, 1993). Nevertheless, the shallow rooting depth of grasses and their ability to grow in cracks in rocks aid in the colonization of these microsites (Mark *et al.*, 1964; Ziemer, 1981). Additional graminoids such as sedges (e.g., *Carex*) and rushes (e.g., *Luzula* and *Juncus*) also colonize cracks and thin soils on a wide range of landslides (Flaccus, 1959; Mark *et al.*, 1964; Elias & Dias, 2009). Graminoids can be important to help stabilize landslides in restoration efforts (Walker *et al.*, 2009; see Chapter 6).

Grasses have both morphological and physiological adaptations to limit water loss. Narrow, strap-shaped leaves enable prolonged exposure to sunlight in relatively dry habitats, and a protective sheath at the base of each leaf helps retain moisture. C_4 grasses are frequently found on

Fig. 4.4. The C_4 grass *Schizachyrium condensatum* on a landslide along the Na Pali Coast, Kauai, Hawaii. Photograph by A.B. Shiels.

tropical landslides (Fig. 4.4), while C_3 grasses dominate temperate landslides (Table 4.3), perhaps because most temperate landslides occur in moist, cooler conditions where C_3 grasses are competitively successful. In the tropics, C_4 grasses tend to dominate in the driest regions. For example, in a large landslide occurring in dry forest in Nicaragua, all of the landslide-colonizing grasses were C_4 (Velázquez & Gómez-Sal, 2007). In the Uluguru Mountains, Tanzania, 10 of the 13 grass species that colonized landslides were C_4 grasses (Lundgren, 1978). In wetter tropical landslides, such as those studied by Restrepo & Vitousek (2001) on the Island of Hawaii, both C_4 and C_3 grass species colonized. Therefore, although C_4 photosynthesis is a more efficient carbon fixing process than C_3 in sunny and dry conditions, it is not a feature of all landslide-colonizing grasses. Clearly, there is a range of adaptations that helps account for successful landslide colonists.

Tropical landslides with bare soils can be quickly covered by grasses. Velázquez & Gómez-Sal (2009b) found that grasses, particularly *Sporobolus indicus* and *Hyparrhenia rufa*, were the dominant initial colonists and persisted as dominants through the first 4 years of succession on a large

Table 4.3. *Grasses (Poaceae) that have been documented in landslides and their photosynthetic pathway*

Location	Annual precipitation (mm)	Species	Carbon fixation process	References
Temperate				
Lake Thompson, New Zealand	2500	*Agrostis parviflora*	C_3	Mark *et al.*, 1964, 1989
		Chionochloa flavescens	C_3	
		Chionochloa conspicua	C_3	
Oregon Cascade Mountains, U.S.	2400	*Agrostis* spp.	C_3	Miles & Swanson, 1986
		Deschampsia elongata	C_3	
		Festuca arundinacea	C_3	
		Festuca occidentalis	C_3	
		Holcus lanatus	C_3	
New Hampshire White Mountains, U.S.	1000–1600	*Agrostis scabra*	C_3	Flaccus, 1959
Andes Mountains, Argentina	3000–4000	*Agropyron* sp.	C_3	Veblen & Ashton, 1978
		Agrostis sp.	C_3	
		Holcus lanatus	C_3	
		Poa pratensis	C_3	
Colorado Rocky Mountains, U.S.	71	*Bromus inermis*	C_3	Langenheim, 1956
		Koeleria cristata	C_3	
		Poa pratensis	C_3	
		Sitanion hystrix	C_3	
		Stipa columbiana	C_3	

Flores Island, the Azores	5632	*Agrostis* sp.	C_3	Elias & Dias, 2009
		Deschampsia foliosa	C_3	
		Festuca francoi	C_3	
		Holcus rigidus	C_3	
		Holcus lanatus	C_3	
Tropical				
Hawaii Na Pali Coast, U.S.	1700–2100	*Chloris virgata*	C_4	A. Shiels, pers. obs.
		Schizachyrium condensatum	C_4	
Hawaii Mauna Loa Volcano, U.S.	2900–4100	*Andropogon virginicus*	C_3	Restrepo & Vitousek, 2001
		Isachne distichophylla	C_3	
		Paspalum conjugatum	C_4	
		Schizachyrium condensatum	C_4	
Luquillo Mountains, Puerto Rico	3000–4000	*Andropogon bicornis*	C_3	Myster & Fernández, 1995;
		Ichnanthus pallens	C_3	Shiels & Walker, 2003; Shiels *et al.*, 2006
		Lasiacis divaricata	C_3	
		Paspalum conjugatum	C_4	
		Paspalum millegrana	C_4	
Blue Mountains, Jamaica	2500–3000	*Chusquea abietifolia*	C_3	Dalling, 1994
		Melinis minutiflora	C_4	
		Zeugites americana	C_3	
Casita Volcano, Nicaragua	1250	*Hyparrhenia rufa*	C_4	Velázquez & Gómez-Sal, 2007
		Panicum maximum	C_4	
		Sporobolus indicus	C_4	

(*cont.*)

Table 4.3. (cont.)

Location	Annual precipitation (mm)	Species	Carbon fixation process	References
Monteverde Cloud Forest, Costa Rica	3300	*Chusquea pohlii*	C_3	Myster, 1993
Uluguru Mountains, Tanzania	950–1920	*Agrostis lachnantha*	C_3	Lundgren, 1978
		Andropogon dummeri	C_3	
		Arthraxon quartinianus	C_3	
		Beckeropsis uniseta	C_4	
		Brachiaria umbratilis	C_4	
		Digitaria velutina	C_4	
		Eragrostis racemosa	C_4	
		Eragrostis schweinfurthii	C_4	
		Hyparrhenia rufa	C_4	
		Panicum trichocladum	C_4	
		Pennisetum purpureum	C_4	
		Rhynchelytrum repens	C_4	
		Sorghum vulgare	C_4	
Andes, Ecuador	800–2000	*Chusquea scandens*	C_3	Stern, 1995a,b

C_3 and C_4 grasses were distinguished based on Edwards & Still (2008), Sage *et al.* (1999), Dengler *et al.* (1994), and Klink & Joly (1989). Poaceae taxonomic classifications have not been updated and reflect the nomenclature specific to each study (e.g., *Rhynchelytrum* is synonymous with *Melinis*; *Panicum maximum* is synonymous with *Urochloa maxima*). All studies were conducted in forest or forest-farmland habitats. Entries are listed in descending order by latitude for both temperate and tropical environments.

landslide in a Nicaraguan dry forest. The prevalence of grasses was particularly high in the slip face and chute of the landslide, and there was little grass colonization in the deposition zone (Velázquez & Gómez-Sal, 2009b). In the upper regions of several Puerto Rican landslides where there was bare soil, Shiels *et al.* (2006) found that the grass *Paspalum millegrana* had 60%–90% germination success within 45 days of sowing seeds. Further experiments revealed that seedling growth, biomass, and survival of *P. millegrana* greatly exceeded a common pioneer forb species, *Phytolacca rivinoides* (Shiels *et al.*, 2006). Bamboo (*Chusquea* spp.) can be a frequent colonist of landslides in tropical America and the Caribbean, yet its relative abundance can vary greatly in the landslide plant community, perhaps because of its rare reproduction via seed (Dalling, 1994; Stern, 1995a,b; Myster, 1997; Kessler, 1999). In Monteverde Cloud Forest Reserve, Costa Rica, for example, *Chusquea pohlii* was the dominant colonist of two landslides (Myster, 1997), and it was also a common early colonist of landslides in Ecuador (Stern, 1995a,b). In Bolivia, *Chusquea* spp. was found in mid- and late-succession on landslides (Kessler, 1999), whereas in Jamaica *C. abietifolia* was only present on one of three $>$ 50 year old landslides (Dalling, 1994), and *Chusquea* spp. was on one of two landslides in Ecuador (Myster & Sarmiento, 1998). Sedges (Cyperaceae) are also common landslide colonists in the tropics; sedges in the genus *Rhynchospora* are found on landslides in both Puerto Rico (Shiels & Walker, 2003; Fig. 4.1) and Jamaica (Dalling, 1994).

Grasses are also common colonists of temperate landslides (Table 4.3). Veblen & Ashton (1978) in Chile found several native and non-native grasses (e.g., *Holcus lanatus*, *Poa pratensis*, *Agrostis* sp.) that frequently colonized landslides. In 9-year-old landslides in New Hampshire, grasses occurred in 45%, and sedges in 65%, of all plots sampled (Flaccus, 1959). However, graminoids were infrequent ($\leq$ 5%) in 30 and 72 year old landslides. Grasses, especially *Deschampsia foliosa* and *Festuca francoi*, dominated vascular plant cover on the upper and middle portions of young landslides in the Azores (Elias & Dias, 2009). *Festuca francoi* was one of the co-dominants in one of two intermediate-aged landslides where rushes (Juncaceae) were also found, and all graminoids comprised little (mean $<$ 5%) of the vegetative cover in the oldest landslides studied in the Azores (Elias & Dias, 2009). Although a variety of graminoids were found on 15–78 year old landslides in Fiordlands, New Zealand, none comprised $>$ 5% of the herbaceous cover (Mark *et al.*, 1964). Therefore, graminoids of both temperate and tropical regions appear readily to colonize landslides but their dominance decreases through time.

However, some grasses may rely on landslide habitats even when their abundance is relatively low, as with the case of the rare New Zealand tussock grass (*Deschampsia cespitosa*) that persists on a prehistoric landslide scar (Mark & Dickinson, 2001).

Largely owing to life history traits such as rapid colonization, vigorous vegetative expansion, and potential dominance, introduced (non-native) grasses have been problematic species in some landslide environments. The non-native African grass (*Hyparrhenia rufa*) was an abundant colonist on a Nicaraguan landslide where Velázquez & Gómez-Sal (2007) suggested that it increases the grass-fire cycle. In two young (4–17 year old) landslides in Hawaii, Restrepo & Vitousek (2001) found two non-native grass species (*Schizachyrium condensatum* and *Paspalum conjugatum*) were abundant colonists. Even after grass removal, many non-native species (including other grasses) returned (Restrepo & Vitousek, 2001). These two examples highlight how substantial shifts in community recovery on landslides can occur from colonization by one or a few non-native species (see Section 5.2.6).

4.5.5 Forbs

Forbs, which are herbaceous seed plants other than graminoids, colonize both temperate and tropical landslides. Where spatial and temporal distributions of forbs on landslides have been examined, they predominate on the slip face and in the chute in early succession, rather than in the deposition zone or later in succession. Typical forbs that colonize landslides include representatives forming nitrogen fixing symbioses (e.g., Fabaceae, *Gunnera*), vines, tall forbs (up to 2 m or more), orchids, and species in the Asteraceae.

The spatial and temporal distributions of forbs on landslides are more likely to be limited by competition than by dispersal. Forbs are well represented in landslide floras because many of them have high rates of seed production and wind-dispersed seeds, as exemplified by species in the family Asteraceae (see below). Often forbs dominate immediately following a disturbance but then are quickly confined to the more erosive surfaces such as the slip face and the chute, where larger, woody plants are less successful. For example, on a single landslide in Glacier National Park, U.S., the forb cover was dense but restricted to the inner (central) portion of the chute (Malanson & Butler, 1984). In Nicaragua, Velázquez & Gómez-Sal (2009b) found that forb cover, including species in the Fabaceae (Table 4.1), initially dominated the chute and deposition zones

of the landslide, but after 2 years the forb cover declined in both of those zones. Grasses, rather than forbs, dominated the slip face on this landslide. Similarly, in New Hampshire, colonizing forbs were found in bedrock cracks in the steepest zones of 9 year old landslides, but forb abundance successively declined in 19, 30, and 72 year old landslides (Flaccus, 1959). *Astelia nervosa*, *Helichrysum bellidioides*, and *Gunnera monoica* (a forb that can have cyanobacteria symbionts in the stems; see Section 4.4), were the most abundant species on the slip faces of the youngest (15 year old) landslides sampled in New Zealand, but were less abundant on 49 and 78 year old landslides (Mark *et al.*, 1964).

Sometimes forbs can be competitively dominant and even increase in cover during succession. In Japan, *Cirsium purpuratum* was one of the dominant pioneers to colonize fresh landslides (Nakamura, 1984), while *Nepsera aquatica* and *Sauvagesia erecta* initially dominated a Puerto Rican landslide immediately following a fire (Walker & Boneta, 1995), and forbs comprised 63% of the vegetation cover on 22 recent (14 month old) landslides in Puerto Rico (Shiels *et al.*, 2008). When forbs form dense thickets, they can inhibit the establishment and growth of other species. In Nicaragua, the annual forb *Tithonia rotundifolia* developed high cover in the landslide chute where it probably inhibited germination of other species (Velázquez & Gómez-Sal, 2009b). In Puerto Rico, dense thickets of forbs inhibited forest development (Walker *et al.*, 2010a). Forb cover may also increase with time since disturbance. Pandey & Singh (1985) did not distinguish between grasses and forbs but found that the herbaceous layer increased approximately tenfold during a 90 year chronosequence study in temperate oak forests in the Himalayas. Consequently, forbs vary from < 5% of vegetation cover in the Azores (Elias & Dias, 2009); to intermediate levels of 10%–35% in New Zealand (Mark *et al.*, 1964) and volcaniclastic soils in Puerto Rico (Shiels *et al.*, 2008); to at least 50% on a different set of Puerto Rican landslides (Myster & Fernández, 1995).

Vines can represent a substantial portion of forb cover on landslides. For example, vines accounted for approximately 75% of the forb cover on eight recent Puerto Rican landslides with volcaniclastic parent material (Fig. 4.5), yet just 10% of forb cover on 22 landslides with dioritic parent material (Shiels *et al.*, 2008). Also in Puerto Rico, the vines *Ipomea* spp. and *Cissus sicyoides* colonized landslides after fire (Walker & Boneta, 1995). In Japan, *Clematis stans* was a common landslide colonist, especially in convex microhabitats where little post-landslide plant damage occurred from burial by rock and falling gravel (Nakamura, 1984). Some vines, such as *Rubus* spp. and *Lonicera japonica*, can form dense thickets on

Fig 4.5. Vines comprise the dominant cover on some recent (<1 year old) landslides in Puerto Rico. Photograph by A.B. Shiels.

landslides that are nearly impenetrable (Hull & Scott, 1982). If the vine is woody (i.e., producing secondary growth) it is called a liana, such as *Smilax melastomifolia* growing on old (130 year) landslides in Hawaii (Restrepo & Vitousek, 2001). Because landslide vegetation generally lacks substantial vertical structure early in succession, most vines that colonize landslides are prostrate or restricted to growing on remnant stems that survived the landslide or on new landslide colonists. The rapid growth rates of vines on landslides can extend over rock surfaces and reduce post-landslide erosion by entrapping litter and soil and reducing their down slope movement (Hull & Scott, 1982; Fig. 4.5).

Large forbs that reach 2 m tall can colonize landslides in both temperate and tropical locations (Lundgren, 1978; Malanson & Butler, 1984; Walker *et al.*, 2010a). For example, species in the genus *Phytolacca* become established early on landslides in Puerto Rico (Fetcher *et al.*, 1996; Shiels *et al.*, 2006) and in Tanzania (Lundgren, 1978). Additionally, in temperate landslides in the Rocky Mountains, U.S., *Heracleum lanatum* and *Veratrum viride* are 2 m tall forbs that dominate the herbaceous plant community (Malanson & Butler, 1984). Without protective bark and woody stems

and branches, such large forbs would seem vulnerable to herbivore attack. However, *H. lanatum*, *V. viride*, and *Phytolacca* spp. have toxins that help defend against herbivores (Malanson & Butler, 1984; Ravikiran *et al.*, 2011). In addition to chemical defenses, physical defenses occur among forbs on landslides. Stinging nettle (*Urtica dioica*) is a common landslide colonist in Glacier National Park, and it has leaf hairs (trichomes), which contain stinging toxins and deter herbivores (Malanson & Butler, 1984). *Urera baccifera*, which is a shrub that is also in the nettle family (Urticaceae), has similar defensive properties and it colonizes landslides in Puerto Rico (Myster & Walker, 1997). Additional physical defenses and anti-herbivory traits found in herbaceous species include silica deposits in the leaves and stems, pubescence, and sticky or glandular excretions in some landslide-colonizing grasses such as *Melinis minutiflora* (Dalling, 1994).

Trapping and digestion of animals can be another adaptation of forbs to obtain limiting mineral nutrients in landslides, particularly in acidic and nitrogen limited microsites. The insect-trapping plant *Drosera rotundifolia* (honeydew) was found in rock cracks and crevices that contained saturated sediments on landslides in New Hampshire (Flaccus, 1959). In the nutrient-poor landslide environments, physical adaptations for both nutrient acquisition and retention appear important to survival of forbs that colonize landslides.

Orchids are occasional colonists of tropical landslides. Orchid cover constituted < 5% of the vegetation cover in 10 year old landslides in both Ecuador (Myster & Sarmiento, 1998) and Puerto Rico (Walker *et al.*, 2010a). Similarly, the non-native orchid *Arundina graminifolia* invaded 4–17 year old landslides in Hawaii where it commonly resprouted after above-ground biomass was removed (Restrepo & Vitousek, 2001). In a study of seven Jamaican landslides, orchids were only present on one 50 year old landslide (*Phaius tancarvilleae* and *Stelis micrantha*; Dalling, 1994). In montane forests in Central America, the orchid *Epidendrum radicans* can dominant roadside landslides (Wolfe, 1987; J. Dalling, pers. comm.). Orchids do not appear to be early colonizers of landslides initially as indicated by their absence from 1 year old landslides in Puerto Rico (Shiels *et al.*, 2008) and Hawaii (A. Shiels, pers. obs.). The scarcity of orchids on landslides may be due to a lack of mycorrhizal symbionts needed for most orchids to establish (Lambers *et al.*, 1998). In addition, most landslide habitats may be too dry for successful orchid establishment. Although many orchids utilize the water efficient CAM photosynthetic pathway, the two orchids commonly found on 4–17 year old landslides

in Hawaii and Puerto Rico (*Spathoglottis plicata* and *A. graminifolia*; Restrepo & Vitousek, 2001; Walker *et al.*, 2010a) both have the C_3 pathway (Goh *et al.*, 1977). Bromeliads (Bromeliaceae) do, however, have CAM photosynthesis, and have been reported on tropical landslides in Bolivia (Kessler, 1999) and Jamaica (Dalling, 1994).

One of the most well-represented plant families among landslides is the Asteraceae. Adaptations for wind dispersal, such as small achenes that are assisted by a hairy pappus, are common among many species in the Asteraceae and these features have likely facilitated seed arrival into landslide gaps (Myster & Sarmiento, 1998; Shiels & Walker, 2003). Other Asteraceae are adapted for epizoochory, as evident with the awns in *Bidens* spp., which are found in 15 year old landslides in Jamaica (Dalling, 1994). In two 10 year old Ecuadorian landslides, the dominant seed rain and the seedlings that emerged from the landslide seed bank were Asteraceae, including *Vernonia patens*, *Hieracium* spp., *Baccharis latifolia*, and *Elephantopus mollis* (Myster & Sarmiento, 1998). *Elephantopus mollis* was also found in the seed rain and established on three of six landslides surveyed in Puerto Rico (Shiels & Walker, 2003). In Jamaica, nearly half of the 23 forb species documented across seven landslides were Asteraceae, including *Baccharis scoparia*, *Bidens shrevei*, *Erigeron karvinskianus*, *Eupatorium* spp., *Gnaphalium americanum*, *Lapsana communis*, and *Vernonia pluvialis* (Dalling, 1994). Similarly, in New Hampshire, *Aster acuminatus* had the highest presence of all herbs (86% of all landslides), whereas several other Asteraceae were also common, including *Anaphalis margaritacea* (77%) and *Solidago graminifolia* (59%) (Flaccus, 1959). Therefore, forb colonists in the Asteraceae are common in a variety of different types and ages of landslides, and, like most other forbs, are particularly successful colonists of the slip face and chute of landslides.

4.5.6 Woody angiosperms

Woody angiosperms dominate the vegetation of many temperate and most tropical landslides (Table 4.2). Some species colonize immediately after landslide formation, while others do not appear on landslides until much later in succession and replace early colonists such as grasses or forbs. Woody angiosperms rarely colonize the slip faces, but are often found in chutes, and are most abundant in deposition zones and landslide edges (Malanson & Butler, 1984; Guariguata, 1990). Woody angiosperms on landslides may or may not resemble adjacent vegetation on undisturbed slopes. Their success on landslides can be attributed to a variety

of traits, depending on the species, including their superior competitive abilities (particularly to shade out competitors of smaller stature); their drought tolerance (from extensive root systems, deciduousness, and reduced water loss from thick or small leaves); their resistance to herbivory; widespread dispersal through light seeds, animal vectors, or vegetative expansion; and the ability of some to establish nitrogen fixing symbioses. We discuss how these traits and others permit successful colonization of landslides by woody angiosperms. We begin with shrubs (< 4 m tall; Arno & Hammerly, 1984), then cover tropical trees, and finally temperate trees.

Shrubs can become relatively abundant on landslides after several years of herbaceous dominance (Sakai & Ohsawa, 1993; Kessler, 1999), and they can occupy all landslide zones and establish dominance near the edges (Malanson & Butler, 1984), the slip face, or the chute (Mark *et al.*, 1964). In moist oak forests in the Himalayan Mountains, India, shrubs appeared 6 years after a landslide had occurred (Pandey & Singh, 1985). On a 2 year old Rocky Mountain landslide, *Amelanchier alnifolia* and *Cornus stolonifera* were the most abundant shrubs (Malanson & Butler, 1984). Veblen & Ashton (1978) determined that the most common shrubs to colonize landslides in Chile immediately after the 1960 earthquake were *Baccharis* spp., which belongs to a genus of (mostly herbaceous) landslide-colonizing species in the Asteraceae (Dalling, 1994; Myster & Sarmiento, 1998). On tropical landslides, shrubs in the Melastomataceae, particularly those in the genus *Miconia*, are among the first woody plants to colonize and can spread and persist for several years (Myster, 1993; Meyer & Florence, 1996; Walker *et al.*, 2010a; see Section 5.2.6). Some genera of landslide-colonizing shrubs are found in both temperate New Zealand and tropical Hawaii, such as *Leptecophylla* and *Coprosma* (Mark *et al.*, 1964; Restrepo & Vitousek, 2001). *Leptospermum scoparium* was the most common shrub colonizing landslides on slip faces of landslides in Fiordland, New Zealand (Mark *et al.*, 1964). *Leptospermum scoparium* is very drought tolerant, surviving in some areas with < 620 mm of annual rainfall. Similarly, *Dodonaea viscosa* survives well in dry areas and grows as a shrub on landslides in Hawaii (Restrepo & Vitousek, 2001), yet it grows as a tree in some less disturbed sites in Hawaii (Wagner *et al.*, 1999) and on 15 and 50 year old Jamaican landslides (Dalling, 1994).

Perhaps the most ubiquitous genus of landslide-colonizing shrubs is *Rubus*; it colonizes temperate landslides in the U.S. (Flaccus, 1959; Hull & Scott, 1982; Malanson & Butler, 1984; Miles & Swanson, 1986), the Azores (Elias & Dias, 2009), New Zealand (Mark *et al.*, 1964), and

Chile (Veblen & Ashton, 1978), as well as tropical landslides in Hawaii (Restrepo & Vitousek, 2001), Jamaica (Dalling, 1994), Puerto Rico (A. Shiels, unpublished data), and Tanzania (Lundgren, 1978). Species in this genus can colonize within 6 months of landslide formation (Lundgren, 1978) and persist for over 50 years (Mark *et al.*, 1964; Dalling, 1994). Some species of *Rubus* form thickets, while most spread through vegetative reproduction in addition to sexual reproduction (Hull & Scott, 1982; Miles & Swanson, 1986; Wagner *et al.*, 1999). Their persistence on landslides may also be due to an abundance of prickly physical defenses.

Ericaceae is another common family that colonizes landslides, with representatives as both shrub and tree growth forms. *Vaccinium meridionale* was a tree found on all seven 15 and 50 year old landslides in Jamaica, and *Lyonia octandra* and *Rhododendron arboreum* were additional tree species in the Ericaceae found on some of the landslides (Dalling, 1994). *Vaccinium cylindraceum* was also found in old landslides in the Azores (Elias & Dias 2009); and in Hawaii, *V. calycinum* was present in initial landslide sampling but the species was absent during the following year of sampling (Restrepo & Vitousek, 2001). In a temperate landslide in the Rocky Mountains, *V. scoparium* appeared in 13 of 20 plots and *V. globulare* appeared in 5 of the 20 plots; *Arctostaphylos uva-ursi* was a less common member of the Ericaceae that appeared in just 2 of the 20 plots (Malanson & Butler, 1984). *Gaultheria shallon* is a dense shrub that appeared in 22% of the plots surveyed on landslides in the Oregon Cascades, yet comprised just 7% cover (Miles & Swanson, 1986). Landslide colonists in the Ericaceae may greatly benefit by forming symbioses with ericoid mycorrhizae, which flourish in nutrient impoverished soils. Ericoid mycorrhizae are able to degrade organic matter to access nitrogen, including absorbing whole amino acids, which can ultimately improve plant nutrition (Read, 1996; Hodge *et al.*, 2000).

The Rubiaceae is generally considered a tropical/subtropical plant family and is well represented on tropical landslides, including those in Jamaica (Dalling, 1994), Puerto Rico (Myster & Walker, 1997; Walker *et al.*, 2010a), Costa Rica (Myster, 1993), Hawaii (Restrepo & Vitousek, 2001), and Tanzania (Lundgren, 1978). The dominant tree genera in the Rubiaceae on these tropical landslides include *Psychotria* and *Palicourea* (Myster, 1993; Dalling, 1994; Myster & Walker, 1997; Walker *et al.*, 2010a). Interestingly, native members of the Rubiaceae are also represented on landslides in both New Zealand and Oregon (Mark *et al.*, 1964; Miles & Swanson, 1986). In New Zealand, there were seven species of *Coprosma* found on a range of surface ages (15, 49, and 78 years old)

and in both slip face and deposition zone microsites (Mark *et al*, 1964). In Oregon, 41% of the sampling plots among 25 landslides had *Galium* spp. (Miles & Swanson, 1986). Although most landslide colonists in the Rubiaceae are trees and shrubs, *Galium* spp. in Oregon and *Anthospermum herbaceum* and *Rubia cordifolia* in Africa are herbaceous.

A great diversity of tree species colonize landslides (Table 4.2), including both gymnosperms (see Section 4.5.3) and angiosperms. Trees are the tallest of all woody life forms, and they can be successful landslide colonists for years when they overtop all other vegetation. Like shrubs, trees can colonize landslides at all stages of succession. Tree seedlings may arrive in the first years following landslides and dominate after 5–10 years in both tropical and temperate environments (Garwood *et al.*, 1979; Miles & Swanson, 1986; Myster & Walker, 1997; Velázquez & Gómez-Sal, 2008). Adaptations by some landslide-colonizing trees to dry habitats such as the Casita landslide in Nicaragua (Velázquez & Gómez-Sal, 2008), may include C_4 or CAM photosynthesis. Two genera with both shrubs and trees that have C_4 photosynthesis include *Chamaesyce* and *Euphorbia* (Batanouny *et al.*, 1991). Trees that utilize CAM photosynthesis, such as members in the genus *Clusia* (Ting *et al.*, 1987), also colonize landslides (Myster, 1993; A. Shiels, pers. obs.). Species of *Clusia* are similar to most bromeliads because their early life stages are epiphytic, typically requiring a host tree for initial colonization, and therefore are unlikely to colonize landslides early in succession.

One of the well-studied tree genera found in tropical disturbances is the angiosperm *Cecropia* (Brokaw, 1998; Shiels, 2006; see Fig. 5.4). In addition to landslides, *Cecropia* rapidly colonizes soil pits created by treefalls (Walker, 2000) and the forest understory following hurricanes (Guzmán-Grajales & Walker, 1991; Shiels *et al.*, 2010). *Cecropia* has many r-selected traits, such as fast growth rates and time to reproduction, small seeds, low resistance to wind disturbance, and shade intolerance (Brokaw, 1998; Walker, 2000). Unlike most r-selected species, *Cecropia* has large leaves; however, the leaves can be slightly to greatly dissected, which is an adaptation for reducing water loss. On tropical landslides in both Puerto Rico and Costa Rica, *Cecropia* is co-dominant with trees and shrubs in the Rubiaceae (Myster, 1997; Myster & Walker, 1997; Table 4.2). A viable seed bank allows for rapid colonization following hurricane disturbance for both *Cecropia schreberiana* and *Psychotria berteriana* in Puerto Rico (Shiels *et al.*, 2010), and the presence of a seed bank in the deposition zone of Puerto Rican landslides may also aid in the establishment of both *C. schreberiana* and *Psychotria* spp. on landslides (Guariguata, 1990).

Trema is a New World and Old World tropical tree genus that readily colonizes landslides in Central America (Garwood *et al.*, 1979; Velázquez & Gómez-Sal, 2008; Pizano *et al.*, 2011) and Pacific islands (Taiwan, J. Dalling, pers. comm.; Hawaii, A. Shiels, pers. obs.). In Panama, Garwood *et al.* (1979) determined that *T. micrantha* became the dominant species within 8 months on a 2 ha earthquake-triggered landslide because it accounted for 66% of all species present. Similarly, Velázquez & Gómez-Sal (2008) found that *T. micrantha* established dominance within 3 years on a rainfall-triggered landslide that was 3 km long and passed through dry forest and farmland in Nicaragua. *Trema*'s successful colonization of recently disturbed habitats is likely due in part to relatively small and slightly thickened leaves, which deter herbivores because they are rough or pubescent, and small fleshy-fruited seeds that facilitate dispersal by birds (Wagner *et al.*, 1999).

The genus *Alnus* (Betulaceae) is an important colonist of tropical and temperate landslides, and it can become a dominant or co-dominant tree on many landslides (Malanson & Butler, 1984; Miles & Swanson, 1986; Kessler, 1999; Geertsema & Pojar, 2007; Table 4.2). Wind-dispersed seeds, enhanced seedling establishment on mineral soils, and rapid growth rates in temperate (Miles & Swanson, 1986; Haeussler *et al.*, 1995; Geertsema & Pojar, 2007) and tropical (Kessler, 1999; Russo, 2005) ecosystems contribute to its successful establishment in disturbed habitats. The genus is well known for its important symbiotic relationship with the nitrogen fixing bacteria *Frankia*, which reside in the root nodules (see Section 4.4; Table 4.1), as well as its important association with mycorrhizal fungi (Russo, 2005). In addition to improving landslide soils by nitrogen fixing symbiosis, *Alnus* may also improve soil fertility by seasonally shedding its nitrogen-rich leaves into the disturbed site (Fig. 4.6). Deciduousness is an adaptation for avoiding low water availability and leaf damage due to freezing. Recovery of *Alnus rubra* on both landslides and logged areas in British Columbia, Canada, was rapid relative to the dominant conifers (*Tsuga heterophylla* and *Picea sitchensis*) of the adjacent forest (Schuster, 2001). Owing to its rapid colonization of disturbed habitats such as landslides, as well as its deciduous and nitrogen fixing symbiotic properties, *Alnus* spp. may also provide favorable habitat for soil-, litter-, and leaf-colonizing animals.

Betula is in the same family as *Alnus*, yet lacks nitrogen fixing symbionts (Soltis *et al.*, 1995). However, the functional role of *Betula* is similar to *Alnus* because both are relatively shade intolerant and wind dispersed (Carlton & Bazzaz, 1998), they both form ectomycorrhizae with

Fig. 4.6. A grove of leafless *Alnus rubra* trees (winter scene) growing on a rotational sediment slump in coastal Oregon, U.S. Photograph by A.B. Shiels.

wind-dispersed basidiomycete fungi (Russo, 2005), and they can establish on landslides quickly and persist as a dominant or co-dominant (Flaccus, 1959; Van der Burght *et al.*, 2012; Table 4.2). On a large rockslide in Switzerland, *Betula pendula* was a dominant tree species that grew larger in exposed microhabitats characterized by boulders than on finer-grained substrates (Van der Burght *et al.*, 2012). In New Hampshire, two species of *Betula* (*B. papyrifera* and *B. lutea*) were the dominant pioneer species 9 years after landslide formation, and both persisted as co-dominants through at least 30 years of succession (Flaccus, 1959). These same two species of *Betula* also dominated early succession on treefall mounds, pits, and forest gaps in the same region in northeastern U.S. (Carlton & Bazzaz, 1998).

Populus tremuloides (Salicaceae) can be a dominant colonist of landslides in montane temperate zones (Mitton & Grant, 1980; Malanson & Butler, 1984; Table 4.2) and is the most widespread deciduous tree in North America. Its vigorous vegetative reproduction enables a single clone to cover many hectares (Mitton & Grant, 1980). Malanson & Butler (1984) found that the dominant tree on a Rocky Mountain landslide was *P. tremuloides*, and that, while it initially colonized the relatively bare

portions of the landslide, it also spread to the forest–landslide edge. The ability of *Populus* spp. to form ectomycorrhizae with air-dispersed fungi facilitates its colonization of bare portions of landslides, and such ectomycorrhizae affiliations allowed *Populus* spp. to colonize buildings wrecked by war in Poland (Dominik, 1956; Vittoz & Hacskaylo, 1974). Additional colonists of Rocky Mountain landslides included members of the genera *Acer* and *Alnus* (Malanson & Butler, 1984), and these genera were also represented on most landslides sampled in the Cascade Mountains (Miles & Swanson, 1986) and on a large rockslide in the Swiss Alps (Van der Burght *et al.*, 2012). *Populus tremuloides* and *Salix bebbiana* were frequent landslide colonists in the White Mountains (Flaccus, 1959), and *S. bacco* was the dominant tree colonist in central Japan (Nakamura, 1984). Like *Populus* spp., *Salix* spp. have wind-dispersed seeds and successfully reproduce vegetatively.

Nothofagus is a genus of landslide-colonizing trees that naturally occurs in the southern hemisphere, and it often dominates forests in less disturbed habitats in New Zealand, Chile, and Argentina. *Nothofagus dombeyi* was the most common tree that colonized Chilean landslides in 1960, and it established in both bare and rocky debris sites (Veblen & Ashton 1978; Table 4.2). In New Zealand, Mark *et al.* (1964) found that *N. menziesii* forests are the climax forest species, yet where such forests surrounded a series of 15–78 year old landslides, *N. menziesii* was a minor component of the vegetation, particularly on the 15 year old landslide. Instead, *Leptospermum scoparium*, in both shrub and tree forms, dominated the New Zealand landslides (Mark *et al.*, 1964). After *N. dombeyi*, the next most common tree on Chilean landslides was *Weinmannia trichosperma*, which is also an evergreen tree that is native to Chile and Argentina. In addition to *N. menziesii*, a southern hemisphere species of *Metrosideros* (*M. umbellata*; Myrtaceae) was found in low abundance on the same landslides in New Zealand (Mark *et al.*, 1964). However, *M. polymorpha* is the dominant native tree in much of Hawaii, and Restrepo & Vitousek (2001) found that it was the most abundant tree that colonized landslides > 4 years old (Table 4.2). Therefore, landslide colonists may be the dominant tree species in the forest that surrounds a landslide (e.g., Veblen & Ashton, 1978; Miles & Swanson, 1986; Restrepo & Vitousek, 2001), or they may be uncommon in the surrounding forest (e.g., Mark *et al.*, 1964; Malanson & Butler, 1984; Nakamura, 1984). In the latter case, landslides promote regional biodiversity (Moss & Rosenfeld, 1978).

In summary, most plant life forms may be represented within the landslide community shortly after disturbance. In the most extreme

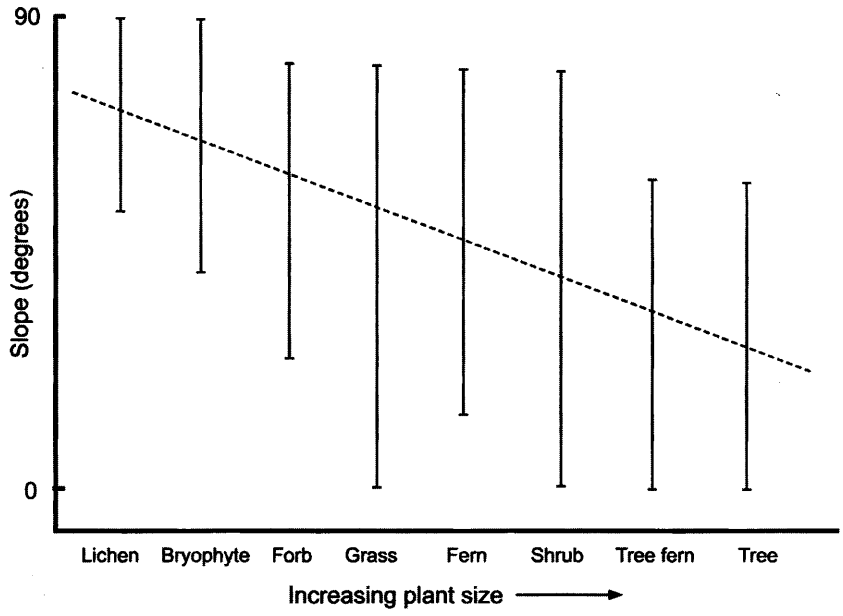

Fig. 4.7. Plant groups on landslides separated by the degree of slope they commonly colonize. The dashed line represents an overall estimate in the relationship between slope and plant size. The presence at some slopes may represent preferred habitat or reflect remaining habitat left by other dominant plant groups. Lichens are included because they are symbiotic with green algae or cyanobacteria (blue–green algae). Free-living cyanobacteria are present on all types of slopes within landslides.

microhabitats of landslides, which include near-vertical substrates and bare rocks in the slip face portion, lichens and bryophytes are able to colonize and in many cases flourish (Fig. 4.7). Free-living or symbiotic relations that include nitrogen fixing bacteria such as cyanobacteria, *Rhizobium*, and *Frankia*, aid in colonization of landslides by *Gunnera* and woody and herbaceous plants, as well as lichen and bryophyte establishment and survival. Mycorrhizal fungi also aid in plant colonization in nutrient depauperate landslide soils. Grasses and ferns colonize all but the steepest, near-vertical, slopes of a landslide and are among the most ubiquitous of all plant life forms that colonize temperate and tropical landslides. The C_4 grasses that colonize tropical landslides are more efficient at carbon fixation in dry habitats; once established, both grasses and ferns successfully spread on landslides through both sexual and asexual reproduction. Forbs are a frequent colonist of all landslides, yet they often play the most important role during early succession in the chute and slip

face of the landslide. The spatial separation of plant groups within landslides may result from both habitat preference and competitive exclusion by other, more dominant species. Woody plants are typically rare on the steep slip face, and many shrubs and trees colonize landslides either early or late in succession and often establish long-term dominance. Herbaceous plants often inhibit other herbaceous plants early in succession, whereas shrubs and trees play a more facilitative role (Gómez-Aparicio, 2009; Walker *et al.*, 2010a). Further discussion of species interactions on landslides occurs in Chapter 5.

4.6 Animals

4.6.1 Invertebrates

Crawling and flying arthropods are probably the first animals to establish on landslides (Hou *et al.*, 2005; Shiels & Yang, unpublished data). Characteristics that likely enhance arthropod establishment on landslides include high tolerance to water and temperature stress (Lavelle & Spain, 2001), as well as the ability to disperse from landslide edges, either by using their appendages or by transport associated with soil and organic matter. Studies of arthropods and other invertebrates are relatively sparse for temperate landslides. However, Růžička and Zacharda (1994) studied arthropod communities on talus slopes in the Krkonoše Mountains of the Czech Republic and found that the most abundant species was a rhagidiid mite (*Evadorhagidia oblikensis*). Additionally, 33 species of spiders (Araneae), 31 species of beetles (Coleoptera), as well as flies (Diptera) and aphids (Aphidinea) were among the most abundant arthropods discovered from year-long pitfall trapping. Stony debris in the talus provided a wide range of temperatures that supported the co-existence of such diverse arthropod communities (Růžička & Zacharda, 1994). Spiders were among the most frequently observed arthropods in the talus slopes of the Niagara Escarpment in Canada (Larson *et al.*, 2000). Based on tropical studies, landslide colonization by arthropods can be rapid; arthropod abundance and richness can reach 6–7 orders and 18–30 families within a few years after a landslide (Myster, 1994), where overall abundances may be comparable to undisturbed forests (Hou *et al.*, 2005; Chien, 2007). Among the most abundant soil arthropods found on landslides as well as in undisturbed forests are mites and springtails (Collembola), and they may comprise 86%–90% of the total individuals in the soil-litter community (Hou *et al.*, 2005) and become landslide dominants within 2 years in

Fig. 4.8. A nest of the ant *Wasmannia auropunctata* on a young (< 5 year old) Puerto Rican landslide. Caliper length is about 20 cm. Photograph by A.B. Shiels.

both Puerto Rico (Shiels & Yang, unpublished data) and Taiwan (Hou *et al.*, 2005). Part of the success of such landslide-colonizing arthropods, particularly mites, is reproduction via parthenogenesis, when unfertilized eggs develop into new individuals (Chien, 2007).

Ants (Hymenoptera) also recruit to disturbed areas, and they can be one of the most abundant colonists in landslides (Myster, 1994) as well as in other newly formed gaps such as those created by clear cuts (Schowalter *et al.*, 1981). In landslides < 2 years old in Puerto Rico, ants extracted from litterbags were the most abundant arthropod observed and were over twice as abundant as on 4–15 year old landslides and in the adjacent forest (Shiels & Yang, unpublished data). The fire ant *Wasmannia auropunctata* appears to be common in young landslides, as indicated by the high abundance in leaf litter and colony nesting on recent Puerto Rican landslides, and because this ant species was not found in any of the nearby forest understory plots (Shiels & Yang, unpublished data; Fig. 4.8). *Wasmannia auropunctata* prefers Collembola, rather than leaf litter, as a food source (B. Edwards, pers. comm.), making it one of the earliest colonizing predators on Puerto Rican landslides. Like most other ground

nesting ants, *W. auropunctata* nest building results in substantial soil mixing within landslides (A. Shiels, pers. obs.). *Wasmannia auropunctata* has invaded disturbed sites in many tropical and subtropical regions outside of its native range of Central and South America, and the human and ecological threats that it poses have resulted in its being listed as one of the world's 100 worst invasive species (Lowe *et al.*, 2000). Additional landslide-colonizing ants may play important roles as seed predators. Ants fed on *Cecropia schreberiana* seeds when offered multiple seed species in landslide feeding trials (Myster, 1997), and ants were observed taking seeds of *Clusia rosea* from beneath perches placed on landslides (Shiels, 2002).

Through insect censuses on 5–20 year old landslides in Puerto Rico and Costa Rica, Myster (1994) found that insect abundances within landslides from two tropical sites were similar, and that flying insects (nectivorous midges and gnats) were the most abundant insects. Additional non-nectivorous insects that are common to landslides in both Costa Rica and Puerto Rico include ants, beetles, flies, and thrips (Thysanoptera) (Myster, 1994), yet each of these insect groups accounted for just 1%–3% of the total animals on landslides in Taiwan (Hou *et al.*, 2005). With insects establishing on landslides relatively early after disturbance, it would seem reasonable that spiders, a common insect predator, would also establish. Spiders did not appear in ground samples from recent (1–2 year old) landslides in Puerto Rico, but did appear in some 4–5 year old and 14–15 year old landslides (Shiels & Yang, unpublished data). Perhaps the absence of spiders on young landslides in Puerto Rico is a reflection of a lack of vegetation complexity for web-building spiders, or simply a result of a sampling bias where only ground-dwelling arthropods were captured. The relatively rapid recovery of litter arthropods in the study by Hou *et al.* (2005) may have also resulted from partial sampling bias because findings were based on small landslides (approximately 50 m^2) that had patches of residual forest soil.

Aerial and arboreal insects, although poorly studied on landslides, can play an important role in nutrient cycling on landslides when they consume plants. For example, Myster (2002) found that 25%–34% of the leaf area of the nitrogen fixing *Inga vera* tree experienced herbivory on Puerto Rican landslides. Aerial insects can also be important pollinators of landslide-colonizing plants. On a large (25 km long) landslide created by Mount St. Helens' eruption in Washington, Dale (1986) measured bumblebee (*Bombus* spp.) visitation to *Lupinus latifolius*, which was an early plant colonist with a *Rhizobium* symbiont (Table 4.1). *Lupinus*

latifolius requires bumblebees to transfer pollen between plants for seed set (Dale, 1986), and 11 bumblebees from at least two *Bombus* species (*B. occidentalis* and *B. californicus*) were observed flying between and foraging on *L. latifolius* on the landslide. Dale (1986) reasoned that, due to the sporadic plant spacing, the bumblebees might travel at least 1 km to transfer *L. latifolius* pollen and that the below-ground bumblebee nests would have been destroyed in the landslide. However, the blow down area (< 1 km from some parts of the landslide) would have provided important sources of surviving bumblebees (Dale, 1986).

Earthworms are a globally important component of the soil fauna in both disturbed and undisturbed sites; over 4000 species of earthworms have been named (Sims & Gerard, 1985). Earthworms can be less abundant in landslides than adjacent forest understories (Hou *et al.*, 2005), or they can differ in species composition when landslides and adjacent forests are compared (Li *et al.*, 2005). In Puerto Rico, Li *et al.* (2005) found two species of earthworms present, but only one species (*Pontoscolex corethrurus*) was found occupying landslides whereas both *P. corethrurus* and *Amynthas rodericensis* occupied the soil in the forest understory. A possible explanation for this species segregation is that *A. rodericensis* is an anecic earthworm, which means it lives only in the leaf litter and organic-rich soil layer and only eats organic matter. *Pontoscolex corethrurus* is an endogenic earthworm that builds complex lateral burrow systems through all of the soil layers and eats both organic matter and mineral soil (Fig. 4.9). With the paucity of organic matter on landslides, the findings from Li *et al.* (2005) fit the expectation that earthworm colonists in recent landslides were the types that survive by eating soil (endogenic) rather than solely organic matter (anecic). Li *et al.* (2005) also found that earthworm abundances in the landslide soils were positively correlated with soil bacteria, leaf litter, and soil carbon.

There have been few studies of invertebrates larger than earthworms on landslides. Slugs and snails are common in disturbed environments and they frequently colonize rock piles at the bases of rock slides, where they survive largely by feeding upon lichens (Lawrey, 1980; Baur & Baur, 1990). The snail *Chondrina clienta* was the only gastropod that occupied exposed vertical surfaces within talus slopes in Sweden because it survives sudden changes in temperature and feeds exclusively upon lichen that grows in such microhabitats (Baur & Baur, 1990). In tropical environments, some snails exist in higher abundances in gaps (e.g., *Caracolus caracolla* in Puerto Rican rainforests) relative to the undisturbed forest, whereas other snail species are equally abundant in gaps and non-gaps

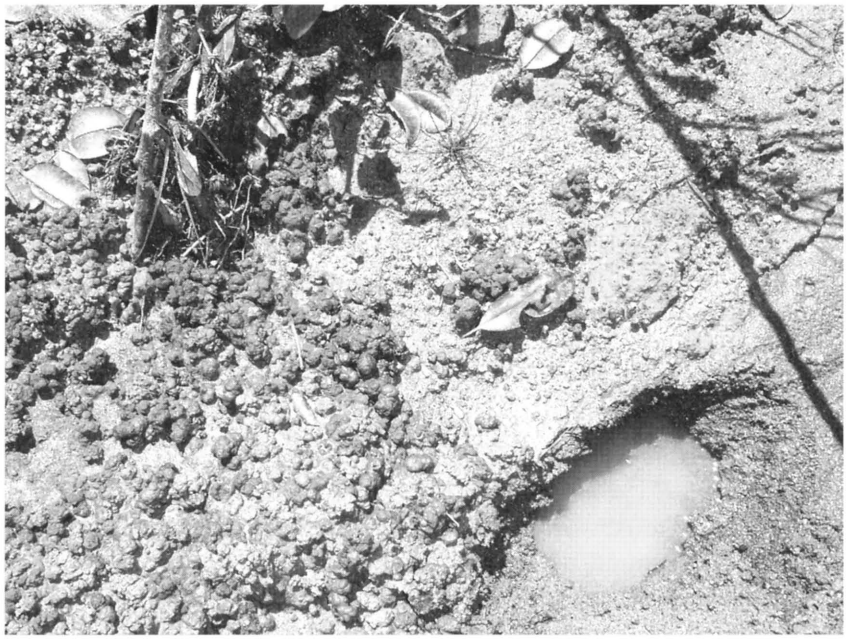

Fig. 4.9. Earthworm castings at the base of a Puerto Rican landslide. Photograph by A.B. Shiels.

(Alvarez & Willig, 1993). Land crabs such as *Epilobocera sinuatifrons* have been observed after heavy rains on landslides in Puerto Rico (A. Shiels, pers. obs.). This particular crab is relatively common in the Puerto Rican rainforest and forages widely from streams and burrows, especially on wet nights (Stewart & Woolbright, 1996). Submarine landslides can be readily colonized by clams in the family Vesicomyidae (e.g., *Calyptogena kilmeri*), which can help date landslides by using growth rates of the clams (Barry & Whaling, 2003). Long-distance displacement of organic matter by turbidity currents likely has an important role in burial of invertebrates living on the sea floor, improvement in nutrient content, and promotion of marine organism diversity and growth (Heezen *et al.*, 1955b; Diaz *et al.*, 1994).

Landslides can also affect down slope ecosystems and the invertebrates that occupy them. In alpine areas in Austria, streams and springs draining from landslides create habitats that can host a variety of aquatic invertebrates (Staudacher & Füreder, 2007). Despite such positive effects of landslides on aquatic invertebrates, landslides are more typically damaging to organisms via sediment deposition (also see Chapter 5; Schuster,

2001; Mackey *et al.*, 2011). While simulating the sediment deposition conditions of a landslide, Norkko *et al.* (2002) found that macrobenthic organisms suffered greatly in estuaries; the numbers of macrobenthic individuals were reduced by 50% after 3 days and 90% after 10 days. Mud crabs (*Helice crassa*), which commonly dig in the benthic zone, were the only animals to emerge from the sediment deposit. Organisms such as bivalves that commonly bed deeply in the sediment suffered the greatest losses (Norkko *et al.*, 2002). Therefore, landslides can greatly affect the invertebrates that occupy the soil, ground surface, and submarine environment, as well as the aquatic organisms that occupy habitats downslope from landslides.

4.6.2 Vertebrates

Birds and small mammals are the dominant vertebrates that generally occupy landslides; however, the initial paucity of vegetation cover and available structure after landslide occurrence generally restricts their use to short visits, especially during early succession. Foraging, perching, courtship, and territoriality are common behaviors of vertebrates on landslides of all ages (Shiels & Walker, 2003; Geertsema & Pojar, 2007).

Gaps with some vegetation can be particularly important for bird visitation (Wunderle *et al.*, 1987). In New Zealand, landslides were apparently important nesting and foraging habitats for the now extinct flightless moa (Wood *et al.*, 2011; Box 4.2). After Hurricane Hugo passed through a Puerto Rican rainforest, the available food sources for birds were largely lost or reduced to gaps containing pioneer vegetation. Such gaps became hotspots for novel bird assemblages, including those bird species that typically occupy the understory or canopy of undisturbed forest (Wunderle, 1995). This behavior was most likely a result of the gaps acting primarily as refuge sites containing some of the only available fruit in the hurricane-affected forest and secondarily as protective sites from predators (Wunderle, 1995). In addition to serving as important forage locations, gaps with emergent vegetation can also be important perches for birds (McDonnell & Stiles, 1983; McClanahan & Wolfe, 1993; Holl, 1998; Shiels & Walker, 2003). The frequency of such perching and feeding behavior on landslides was observed during a 14-month study in which seven species of birds were recorded on artificial perches (4–5 m tall saplings) that were placed on relatively recent landslides (Shiels & Walker, 2003; Fig. 4.2). Another 15 species were recorded either foraging or perching at the landslide–forest edges, or less frequently flying over

Box 4.2 Landslides were refuge sites for moa (prehistoric birds)

The moa were giant flightless birds (some up to 3.5 m tall and 200 kg) that were endemic to New Zealand. Their natural predators were birds of prey, including the impressive Haarst Eagle (*Harpagornis moorei*), which had a 2–3 m wingspan and large (> 10 cm) talons that could crush bone up to 6 mm thick under 50 mm of skin and flesh (Bunce *et al.*, 2005). However, moa were driven to extinction by human hunters shortly following human colonization of New Zealand. Because of their large size, flightless nature, and prehistoric presence, moa have long intrigued archeologists, ornithologists, ecologists, and natural historians. Moa bones recovered during an archeological survey on a large rock fall have recently been used to date the landslide and the rupture of the Alpine fault in New Zealand (Wood *et al.*, 2011). Further surveys by paleoecologists have determined that the remnant rocks in the rock fall provided both shelter and nesting sites, as evidenced by egg shells, bones, and nests, for at least three species of moa from the time of the rock fall until the sites were revegetated with forest when human arrival caused their extinction (J. Wilmshurst, pers. comm). The remains were from three species, the South Island giant moa (*Dinornis robustus*), the upland moa (*Megalapteryx didinus*), and the heavy-footed moa (*Pachyornis elephantopus*). The abundance of moa bones on a single rock fall deposition zone indicates that landslides would have been attractive sites for these large birds, likely because of the abundant vegetation for both forage and cover and the large rock overhangs for shelter. Further excavation uncovering moa coprolites (preserved droppings) from beneath rock overhangs within the rock fall have allowed for reconstruction of the moa diets via pollen analysis, seed identification, and ancient plant DNA (J. Wilmshurst, pers. comm.).

the landslides (Shiels & Walker, 2003). The most common birds observed were gap specialists such as grassquits (*Tiaris bicolor* and *T. olivacea*) and gray kingbirds (*Tyrannus dominicensis*), and forest birds such as tanagers (*Nesospingus speculiferus* and *Spindalis zena*) (Wunderle, 1995; Shiels, 2002; Shiels & Walker, 2003). The only nesting observed in the vicinity of the landslides was by the gray kingbird, which nested on a 10 m tall utility pole (Shiels, 2002). Many island birds that live in areas of high disturbance, including the gray kingbird, are facultatively omnivorous (Waide, 1996; Shiels & Walker, 2003), and therefore may forage within

landslides for fruits, seeds, and arthropods. Rock falls and rotational landslides often form cliffs, which may be colonized by swallows and kingfishers; cliffs may also serve as burrow habitats for seabirds on coastal landslides (Schuster, 2001; Geertsema & Pojar, 2007).

New landslides that contain freshly exposed soil with little vegetation can provide birds with mineral soil used to aid digestion of plant material (i.e., geophagy). On a recent landslide in a montane rainforest in New Guinea, at least four species of parrots, two species of pigeons, one hornbill, one crow, and possibly one cassowary were documented feeding on the bare soil (Diamond *et al.*, 1999). Parrots typically fed on the landslide soil in the morning, while pigeons would frequent the exposed soil in the afternoon. Because of the paucity of landslides in the area, and the relatively long distances that birds would have to travel to get to a landslide, recent landslides with some bare soil appear to be important destinations for many birds in this region. Laboratory tests of the clay-rich soils consumed by the birds revealed a particularly high cation exchange capacity and binding capacity for tannins and quinine. Therefore, Diamond *et al.* (1999) suggested that the consumption of landslide soil by birds in New Guinea served to bind bitter tasting secondary compounds in previously ingested fruit and seed.

Heterogeneous microhabitats within landslides attract many mammals, amphibians, and reptiles. Talus slopes resulting from temperate landslides are used by a variety of amphibians (e.g., tree frogs, toads) and reptiles (e.g., lizards, skinks, snakes) for feeding and reproduction (Maser *et al.*, 1979). More than 60% of the amphibians and reptiles that occur in Oregon and Washington, U.S., utilized talus habitats (Herrington, 1988). Cracks, crevices, and trees on talus slopes were attractive habitats for rodents, voles, and bats (Maser *et al.*, 1979). Insectivorous bats may frequent relatively young landslides because of the open space and presence of aerial insects (Willig & Gannon, 1996), and potentially roost in cliff faces formed by rock falls or rotational landslides (Schuster, 2001; Geertsema & Pojar, 2007). Frugivorous bats commonly visit tropical landslides (Matt *et al.*, 2008). Rodents, which comprise over 40% of the world's mammal species, can be found in a wide variety of habitats and ecosystems that includes landslides (Long, 2008). Rodents have been observed visiting both tropical and temperate landslides (Larson *et al.*, 2000; Shiels, 2002; Geertsema & Pojar, 2007). For example, pikas (*Ochotona princeps*) commonly occur on talus (Hafner, 1993). Additional rodents that occupy temperate landslides include mice and rats (Muridae; Maser *et al.*, 1979), chipmunks, and squirrels (Sciuridae; Matheson, 1995). When ponding results from landslides, beavers (*Castor canadensis*) may colonize

Fig. 4.10. An invasive black rat (*Rattus rattus*) in Hawaii. Note the shiny ear tags. Black rats have been introduced to most islands and continents worldwide. They are known to forage in landslides where they have been recorded as both seed dispersers and predators. Photograph by A.B. Shiels.

(Geertsema & Pojar, 2007). One study in a montane cloud forest in the Chiapas region of southern Mexico sampled rodents on landslides and adjacent undisturbed forest following an El Niño year where 10%–12% of the landscape was affected by landslides (Samaniego-Herrera, 2003). Three species of native rodents (*Peromyscus guatemalensis, P. aztecus*, and *Heteromys goldmani*) were collected from landslides and an additional five rodent species were collected from adjacent forest understories, suggesting that the majority of the rodent species in the Chiapas forest did not frequent landslide gaps (Samaniego-Herrera, 2003). Despite differences in species composition, rodent abundances did not differ along the gradient from landslide to adjacent forest understory, which may benefit rodent predators such as raptors that commonly forage in disturbed areas rather than in the forest understory (Samaniego-Herrera, 2003). Black rats (*Rattus rattus*) have been observed in landslides and adjacent forest in both Puerto Rico and Hawaii (Fig. 4.10; A. Shiels, pers. obs.); this non-native species has invaded most continents and islands and may alter plant communities through both seed predation and dispersal (Shiels, 2011; Shiels & Drake, 2011).

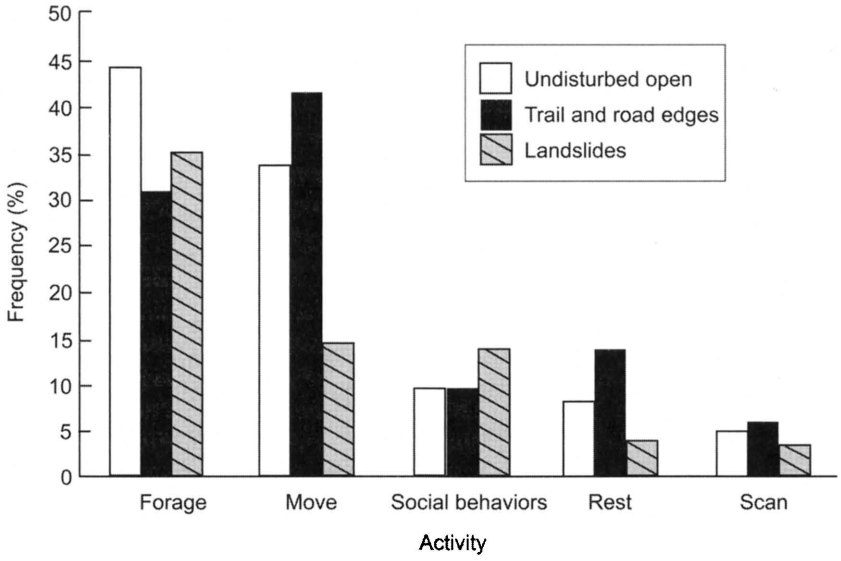

Fig. 4.11. Observed activities of the mountain monkey, *Circopithecus lhoesti*, when it is on the ground in a forest in Rwanda. Social behaviors included play, aggression, and grooming. From Kaplan & Moermond (2000) with permission from Wiley & Sons.

Mammals larger than bats and rodents have been documented on landslides in temperate and tropical ecosystems (Maser *et al.*, 1979; Kaplan & Moermond, 2000). Thirty-six mammal species, including raccoons, porcupines, coyotes, foxes, weasels, badgers, skunks, lynx, bobcat, and bear, were listed as using talus slopes in Wyoming, U.S. (Maser *et al.*, 1979). Bears (*Ursus* spp.) eat emerging graminoids and forbs in landslides, and moose (*Alces alces*) have also left evidence of heavy browsing on landslides (Geertsema & Pojar, 2007). Several non-native mammalian herbivores visit landslides and consume vegetation in New Zealand and elsewhere (Plate 13), including deer (*Cervus elaphus*), goats (*Capra hircus*), and possums (*Trichosurus vulpecula*) (James, 1973). Mountain goats (*Oreamnos americanus*) feed and rest on landslides and mountain slopes during the afternoon and then return to nearby cliffs before dark where fewer predators are present (Geist, 1971). Forest-dwelling monkeys (*Circopithecus I'hoesti*) in Rwanda preferentially visit landslides and other disturbed habitats to forage on the ground for herbaceous plants (Kaplan & Moermond, 2000; Fig. 4.11). Vertebrates visit landslides primarily for forage, yet some also reside on landslides for extended periods of time,

such as when they use landslide microhabitats for nesting and predator escape.

4.7 Conclusions

Biota that disperse onto landslides are generally those that are small (e.g., Fig. 4.1); yet adaptations for wind-dispersal (plants) or appendages for locomotion (animals) enable a greater range of organisms to disperse onto landslides, including those from areas well beyond the adjacent habitats. The majority of landslide colonists are gap-specialists with adaptations to survive in mostly bare, low-nutrient environments where temperature and water stress are commonly experienced. There do not appear to be landslide specialists, or organisms that only colonize landslides. Instead, most landslide-colonizing species occur in other types of recently disturbed habitats; however, in some cases, landslides are also important habitats for late-successional species regeneration. Landslide colonists tend to have life-history characteristics that include high fecundity, small body (or seed) size, reduced time to reproduction, and the ability to disperse widely. Water conservation strategies appear important among landslide-colonizing plants, including small and thickened leaves, deciduousness, and C_4 photosynthesis for many tropical grasses. Plant adaptations to nutrient-poor conditions on landslides include symbioses with microbes, particularly nodular nitrogen fixing bacteria. Lichens represent an additional symbiosis common on the steepest portions of landslides, including rocks and bare soil. The first animals to colonize landslides are soil and litter arthropods, particularly mites, Collembola, and ants. Parthenogenesis facilitates rapid expansion and survival of some arthropods on landslides. Most of the remaining animals that colonize landslides are visitors, rather than residents, at least until sufficient habitat structure has developed. A suite of birds, bats, rodents, ungulates, and monkeys has been observed on landslides. Observed behaviors of such animal colonists have included foraging, nesting, perching or resting, reproduction, geophagy, and playing (monkeys).

Our limited understanding of animal colonists on landslides, and their roles in landslide ecology, represents an area deserving future attention and investigation. In addition to more widely documenting animals that occupy landslides, an understanding of the types and frequencies of biotic interactions will also improve our understanding of landslide ecology. For example, how are the roles of animals as pollinators, herbivores, seed predators, and seed dispersers on landslides different than those in

non-landslide environments? To what extent do such interactions, and additional interactions within the landslide food web, change through succession? Does the success of early plant colonists on landslides reflect their natural independence from mutualisms with animals? For example, many plants are able to self-fertilize, which may, along with frequent asexual reproduction, facilitate dominance on landslides. Lastly, symbiotic relationships are common within landslide biota. The quantity of nitrogen fixed by various symbionts (lichens, root nodules, *Gunnera*, and free-living organisms) needs future investigation, as do the relative effects of such nitrogen fixers on biotic development within landslides. In summary, much more documentation of landslide-colonizing biota is needed, in addition to investigations of how these colonists interact with each other and alter ecosystem functions. Comparisons of the role of microbes, plants, and animals on landslides and non-landslide environments will help explain the importance of landslide habitats across the landscape.